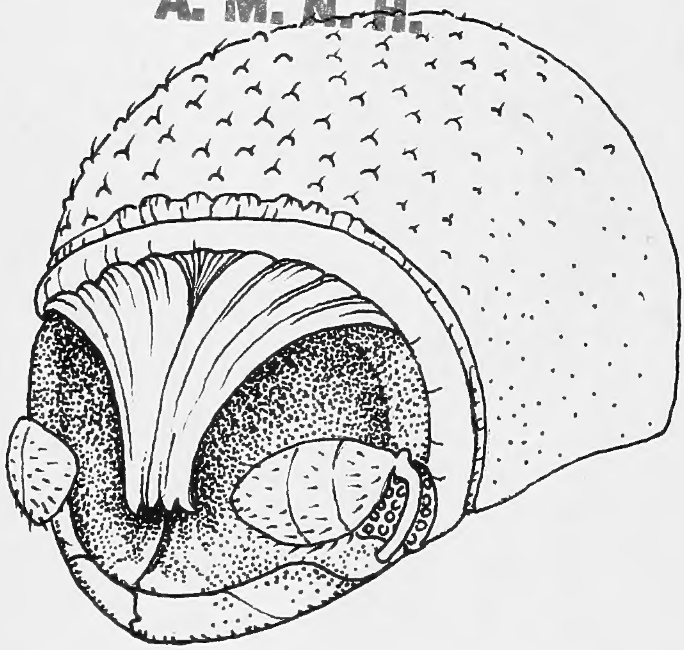
GREAT BASIN NATURALIST MEMOIRS

Number 10 Brigham Young University 1986

A Reclassification of the Genera of Scolytidae (Coleoptera)



GREAT BASIN NATURALIST

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ISSN 017-3614

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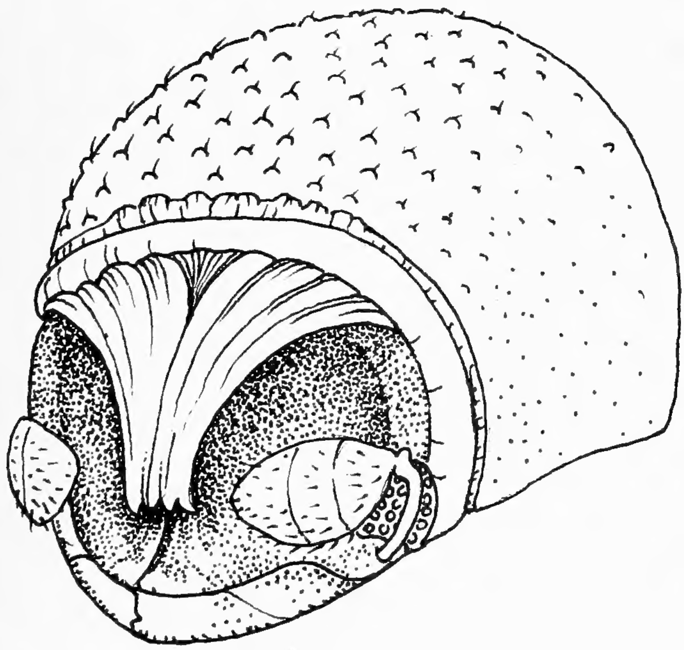


CONTENTS

Great Basin Naturalist Memoirs

A Reclassification of the Genera of Scolytidae (Coleoptera)

No. 10 Brigham Young University, Provo, Utah 1986

Stephen L. Wood[1]

Abstract.— A taxonomic revision of the genera of Scolytidae (Coleoptera) in the world fauna is presented. Included are 215 valid genera and 273 invalid generic and subgeneric names. The type-species for each genus-group name was examined, including the type-specimen of the type-species in those taxa where a holotype, lectotype, or neotype has been designated—with the exception of four contemporary genera, the type-series of which are lost, and six fossil genera for which no effort was made to locate the types. Taxonomic keys to the families of the Curculionoidea, and to the subfamilies, tribes, and genera of Scolytidae are presented. Descriptions and citations of the original validations of the two subfamilies and 25 tribes of Scolytidae are included. For each genus-group name there is a citation of its original validation, type-species, and synonymy. For each valid genus there is an indication of its distribution, the approximate number of valid species, basic feeding and mating habits, and citations of published keys for the identification of species.

Of general interest to coleopterists is a review of the status and position of the families Platypodidae and Scolytidae within the Curculionoidea, including several characters not previously presented. These two families are entirely distinct from one another and from Curculionidae. The phyletic position of Platypodidae and Scolytidae is near the more primitive families of Curculionoidea and quite remote from specialized Curculionidae.

Because of their immense economic impact on world forests, forest products, and certain aspects of agriculture, considerable attention has focused on the Scolytidae. Although the literature is filled with reports of the economic ravages and of efforts made to manipulate their populations, comparatively little attention was given to other aspects of their study prior to 1960. Since then, there has been a virtual explosion of information about many other facets of their existence.

Although advances in basic communication involving nomenclature and classification normally preceded the expansion of knowledge in other groups of organisms, this was not the case with the Scolytidae. There appear to be several reasons for this delay. The sheer number of species and the urgency to do something with the management of populations compelled local foresters to act. The unavailability of trained taxonomists apparently caused practical foresters to enter the fields of naming and identifying species to meet their own limited needs. With two pre-1960 exceptions, taxonomic work on Scolytidae was done by senior foresters who lacked a fundamental interest or training in the study of diversity, phylogeny, or evolution. These exceptions were Chapuis, who produced a classical work on Platypodidae (Chapuis 1865) and was starting to work on Scolytidae (Chapuis 1869) before jurisdictional problems arose, and Hagedorn, whose brief career (1904–1912) ended tragically. The unwillingness to accept and apply the concept of evolution and to abandon the typological (morphological) species concept by more recent influential workers also delayed progress.

The present study had its origin in a conversation with C. D. Michener, at Logan, Utah, in August 1949, during which he suggested a reclassification of the genera of Scolytidae in

[1]Life Science Museum and Department of Zoology, Brigham Young University, Provo, Utah 84602, USA.

the world fauna as an appropriate subject for my doctoral dissertation. Fortunately, for me and for science, a more limited topic was chosen, but the suggestion was never forgotten and has remained a lifelong objective. In 1981, when I was asked by colleagues to finalize a comprehensive world catalog of Scolytidae, completion of the generic study became mandatory and urgent. Although this presentation is a bit premature, its basic objectives are achieved. More thoughtful selection of illustrations and greater detail in their presentation would have been helpful to the user.

The Scolytidae are among the more difficult insects to classify; yet their tremendous economic importance is so great that immediate and precise identification is demanded by those industries threatened by the activities of these insects. Although my attraction to the Scolytidae was to their fundamental structure, diversity, ecology, and behavior from theoretical and other points of view, as knowledge began to accumulate, my rural background and religious philosophy made me sensitive to the economic interests of others and to a need for me to assist them with what I had learned. Another need was also paramount. Among the great frustrations in learning are those resulting from errors that have been transmitted from one generation to the next and, once learned, must be unlearned and corrected before progress can continue. Biological nomenclature and classification have been profoundly impeded in their progress by this problem. Therefore, the primary objectives of this study are (1) to review the holotypes or syntypes of the type-species of all named genera and subgenera to make certain that they are correctly placed in appropriate genera, then find the correct generic names for them, and review as many species as possible and group them in those genera, and (2) to devise a scheme of classification such that others can identify those genera. If these objectives are achieved in at least some measure, it is hoped that the constant name changing and duplication of effort (resulting from synonymy) that has impeded taxonomic progress in my generation will be reduced to a minimum. This classification of categories above the species level will be the framework on which the catalog of species, now in preparation, will be organized.

HISTORY

Linnaeus (1758) included five species of Scolytidae in his Systema Naturae, edition 10, all under the name *Dermestes* (*typographus*, *micrographus*, *poligraphus*, *piniperda*, *domesticus*). Fabricius (1801) expanded this to include 52 species under the generic names *Apate* (5), *Bostrichus* (21), and *Hylesinus* (26). Gemminger and Harold (1872) list 535 species in 60 genera. Hagedorn (1910a, b) lists 1,234 species in 115 genera. There has been no comprehensive classification or catalog of the family on a worldwide basis since the work of Hagedorn, but it is estimated that more than 6,000 biological species are currently recognized. The first generic name erected for a member of this family was *Scolytus* Geoffroy (1762; China 1962, International Commission on Zoological Nomenclature 1963). Since then, 488 generic and subgeneric names have been proposed for the group, of which 215 are treated below as valid.

In an attempt to estimate the number of species remaining to be named from America north of Mexico, White (1975), in his example using Scolytidae, recognized 592 species in 1970 and projected that there would be 650 named by the end-point year of 2040, when 100% would be known. That estimate was made prior to publication of my monograph (Wood 1982). In the monograph, numerous species were placed in synonymy and others were named or they extended their distributions into the United States and Canada, leaving about the same total number of species and projection as before. Meanwhile, more than half of the scolytid fauna of Mexico and Central America was named from 1960 to 1982. This rapid expansion of the fauna south of the United States made a projection for the larger area meaningless at the present time.

Few attempts to classify the higher categories of Scolytidae on a worldwide basis have been published. Perhaps the first contribution worthy of note was that of Ferrari (1867), who listed and described the genera of Tomicides (my Scolytinae with Scolytini deleted). There was no attempt to actually classify the genera by Ferrari. Eichhoff (1878a) published a classical monograph of this same group in which he presented keys and descriptions to all known genera and species. His family

Tomicini included 40 genera that were distributed among the subfamilies Crypturgidae (*Crypturgus, Dolurgus, Aphanarthrum, Triotemnus, Pycnarthrum*), Cryphalidae (*Liparthrum, Hypoborus, Triarmocerus, Cryphalus, Glyptoderus, Stephanoderes, Cosmoderes*), Problechilidae (*Problechilus*), Xyloctonidae (*Xyloctonus, Scolytogenes*), Pityophthoridae (*Pityophthorus, Eidophelus, Taphrorychus*), Tomicidae (*Thamnurgus, Xylocleptes, Tomicus, Lepicerus, Dryocoetes*), Hylocuridae (*Hylocurus*), Micracidae (*Micracis*), Araptidae (*Araptus*), Hexacolidae (*Hexacolus*), Xyleboridae (*Coccotrypes, Xyleborus, Premnobius, Gnathotrichus*), Xyloteridae (*Trypodendron*), Corthylidae (*Corthylus, Brachyspartus, Anchonocerus, Phthorius, Trypocranus, Pterocyclon*), and Amphicranidae (*Steganocranus, Amphicranus*).

Hagedorn (1910a, b) treated 115 genera and 1,234 species in the entire family worldwide. He divided Scolytidae (Ipidae, in his usage) into four non-Linnean subfamilies, based on the detailed structure of the mouthparts, that contained the tribes indicated: Pilidentatae (Phloeotrupinae), Spinidentatae (Eccoptogastrinae, Diamerinae, Crypturginae, Hylocurinae, Hylesininae, Ipinae, Cryphalinae), Saetidentatae (Xyleborinae, Corthylinae), and Mixodentatae (Spongicerinae).

Hopkins (1915a, b), in two papers, (a) reclassified the subfamilies and tribes of Scolytidae and (b) reclassified the genera and species of Cryphalinae. He elevated the group to superfamily rank, Scolytoidea, and recognized four families within it (Ipidae, Scolytidae, Scolytoplatypodidae, and Platypodidae). His Ipidae included the subfamilies Cryphalinae, Ipinae, Micracinae, Webbinae, Xyloctoninae, Crypturginae, Phloeotribinae, Hylesininae, and Phloeoborinae. His Scolytidae included the subfamilies Coptonotinae, Hexacolinae, Bothrosterninae, Camptocerinae, and Scolytinae. His Scolytoplatypodidae included the subfamily Scolytoplatypodinae, and Platypodidae the subfamilies Platypodinae, Genyocerinae, and Chapuisinae. It appears to have been the intention of Hopkins to follow his basic classification with a series of papers treating in detail the various divisions of his classification, but only one paper was published. Hopkins (1915a) reviewed the subfamily Cryphalinae, in which he included 48 genera that are currently distributed (below) among the tribes Cryphalini, Dryocoetini, and Xyleborini.

Wood (1978) reviewed 15 major published classifications of the higher categories of Scolytidae, including all of those cited above, and presented a revised and expanded classification of subfamilies and tribes and tentatively assigned 404 nominate genera and subgenera to his 25 tribes. That classification was adapted to his monograph of the North and Central American Scolytidae (Wood 1982), which listed 1,433 species in 94 genera. The present contribution is an expansion of that classification to the genus level for the entire world.

REVIEW OF CHARACTERS

Characters Shared by Platypodidae and Scolytidae

In the early stages of this study, I was thoroughly convinced that Platypodidae could be no more than a well-marked, primitive subfamily of Scolytidae. Shared characters that led to this premature conclusion included: (1) clearly formed pregular sutures extend from the anterior end of the median gular suture to or near the anterior tentorial pits; these sutures are reinforced internally by a massive internal inflection of the cuticle that occurs nowhere else in the Curculionoidea; (2) the mandible lacks the horizontal cylinder that rotates on the anterior and (heavily reinforced) posterior condyles, with its cutting edge apical; instead, the posterior condyle is in a different position, the axis of the mandibular hinge is transverse, and the cutting edge is mesal (as in Anthribidae and Nemonychidae); (3) the rostrum is short to nonexistent; (4) the tibiae totally lack corbels, but they share a common basic structure and are armed on the apical and lateral margins by a characteristic series of spines; (5) the eyes are essentially flat against the head; (6) the antennae are mostly of the same basic geniculate type, with some members of several primitive tribes having a short scape (little if any longer than the pedicel); (7) the visible abdominal sterna 1 and 2 are weakly connate, except all are free in all primitive genera of Platypodidae; (8) the elytral interstriae 10 ex-

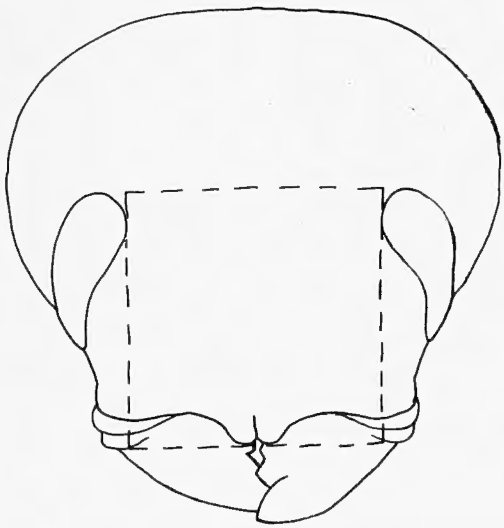


Fig. 1. Outline of cephalic aspect of the head of *Pseudohylesinus sericeus* (Mannerheim), with frontal rectangle indicated by the square of dash lines.

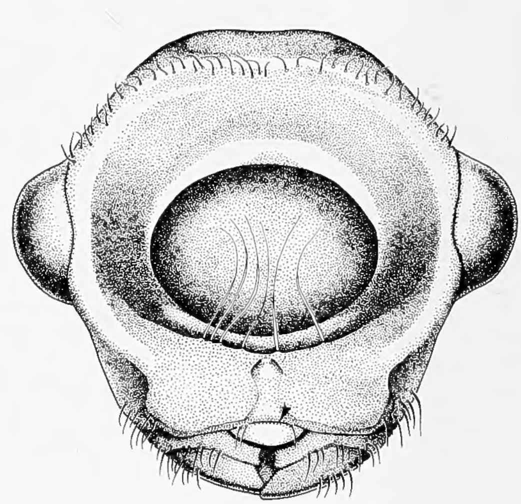


Fig. 2. Cephalic aspect of the head of a female *Chaetastus tuberculatus* (Chapuis) (Platypodidae) showing a conspicuous "labrum" in the median area just below the epistomal margin arrow. (Re-drawn from Strohmeyer (1920: 15, Fig. 5).

tends to near the apex in all Platypodidae and in some primitive representatives of virtually all tribes of Scolytidae; (9) the larval characters are basically the same except as noted below; and (10) they share the same basic ecological niche.

Characters Not Shared with Other Curculionoids

Curculionoidea, excluding Anthribidae, Nemonychidae, Platypodidae, and Scolytidae, share a unique mandibular character in which the basal half forms a cylinder that rotates on a horizontal axis between the two articulating condyles (Fig. 8). The hypostomal area adjacent to the posterior condyle is enlarged and strengthened to accommodate a new mode of action; the cutting edge is apical and usually takes the form of a large cusp on the side of the basal cylinder. In the four families identified above, the mandibular condyles are closer together, the oblique action is more like that of a hinge, the cutting edge is mesal, the mandible ends in an acute point, and the hypostomal area is minimal.

The Anthribidae and Nemonychidae have an adult labrum. It is lost in all other Curculionoidea; however, in most primitive tribes of Scolytidae (most Hylesininae, Ctenophorini, etc.) there is an epistomal lobe that resembles a small, fused labrum and is probably homologous to it (Fig. 1). In Platypodidae the epistomal lobe is more generally present, and in *Tesserocrerus* and *Chaetastus* (Fig. 2) a suture separating this lobe from the epistoma is evident in some species. Comparable structures are unknown in the remainder of the Curculionoidea.

In general, beetles have two gular sutures that are separated by a median gular sclerite. In Nemonychidae (Fig. 3) and some Belidae (Fig. 3B, and Crowson 1967) two gular sutures are clearly indicated from the margin of the foramen magnum to the point of invagination of the tentorium (posterior tentorial pit) where they end. In Anthribidae, the entire tentorial structure is lost and the gular sutures are usually reduced to little more than lateral irregularities on the margin of the foramen magnum. In Belidae there is variation from two widely separated gular sutures that end in two separate posterior tentorial pits (Fig. 3B) to convergence to a single median pit, with consequent reduction in size of the gula, to formation of a single median gular suture of variable length (Fig. 3C). The allies of Belidae (Aglycyderidae and Oxycorynidae including *Rhopalotria*) share at least part of this same variability. The only other known members of the Curculionoidea that share in similar variability are members of the neotropical scolytid genus *Gnathotrupes*. Of the 23 species of

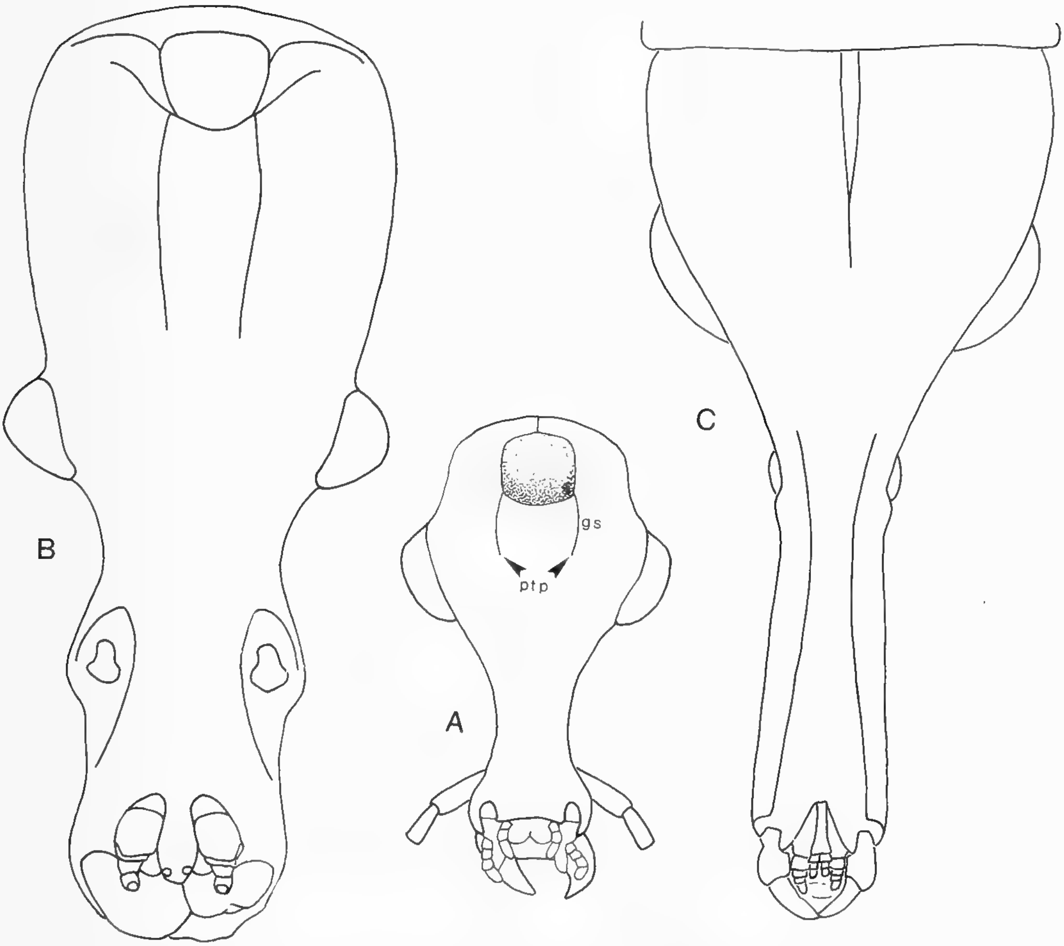


Fig. 3. Diagrams of the ventral surface of the head of (A) *Cimberis attelaboides* (Nemonychidae), (B) *Belus* sp. (Belidae, from Australia), and (C) an unidentified female Belidae from Australia. Note the convergent postgular sutures and remnants of pregular sutures from the level of the antennal insertion to (or toward) the anterior tentorial pits. gs = gular suture, ptp = posterior tentorial pit.

Gnathotrupes examined for this character by me, 5 had two complete gular sutures that extended to and were continuous with the pregular sutures, 8 had the pregula elongated and extending most of the distance to the postgula, and 10 had the pregula more or less normal. Most Platypodidae (Fig. 4) have an unusually large pregula and a short to very short median gular suture.

Pregular sutures are totally absent in all curculionoids, except for Platypodidae (Fig. 4) and Scolytidae (Fig. 5-G) and for their partial presence in females of two (unidentified) Australian Belidae (Fig. 3C). In these two belids the pregular sutures extend only from near the anterior tentorial pits to near the point of antennal articulation; they are not represented from the area of antennal articulation to the anterior end of the median gular suture (the point marked externally where the tentorial apparatus invaginates). The pregular sutures illustrated by some writers on Curculionidae (Hopkins 1911:Fig. 1) do not exist; they represent irregular undulations in the cuticle that serve to strengthen the posterior (or ventral) wall of the rostrum and do not qualify as sutures in any acceptable usage of that term.

Mouthparts have been used extensively in fundamental divisions of the Curculionoidea (Crowson 1967). For example, in Anthribidae and Nemonychidae the maxillary lacinea and

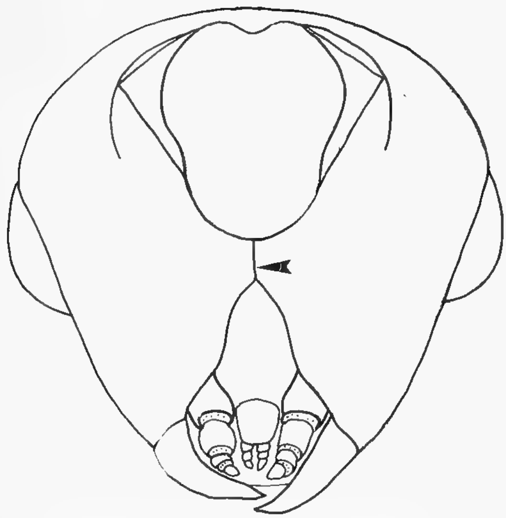


Fig. 4. Posterior aspect of head of a female of *Doliopygus chapuisi* (Duvivier) (Platypodidae). Note the very short median gular suture and the prominent pregular sutures.

galea form separate elements (Ting 1936:Fig. 78). The only other curculionoids sharing this character are the Tesserocerini (Platypodidae) (Fig. 6), Attelabidae, and Rhynchitidae (Ting 1936:Fig. 78). Similarly, the Anthribidae and Nemonychidae have a 4-segmented maxillary palpus (Crowson 1967, Ting 1936). This character is shared by all Attelabidae (Crowson 1967, Ting 1936), some Rhynchitidae, and one Platypodidae (*Austroplatypus*) (Browne 1971a).

The costate lateral margins of the pronotum in primitive tribes of Scolytidae (Diamerini, Ctenophorini, Scolytini, etc.) is another indication of primitive origin of this family within the Curculionoidea.

The tibial structure of Platypodidae and Scolytidae is unique. It appears to have been derived from a structure resembling that of *Protohylastes* (Fig. 7), in which the median member of three apical spines became the terminal mucro of Platypodidae and the mesal spine became the terminal mucro in Scolytidae (Wood 1973a). The lateral margin is armed by one or more spines in primitive tribes; these may be replaced in specialized groups by socketed denticles (teeth) of setal origin (Wood 1978). The tibial structure of *Scolytus* and *Camptocerus* is a specialized deviation from the basic scolytid structure that only superficially resembles the cossonine tibia. Similar structure occurs in Histeridae, Bostrichidae, Brenthidae, or other coleopterous groups having a long history of occupancy of insect tunnels bored in wood. The tibial spines of Araucarini (Cossoninae) that have been suggested as ancestral to those of Scolytidae (Kuschel 1966) also are of independent origin; in fact, the scolytid denticles to which they were compared are socketed and bear no structural similarity to them whatever.

The elytral locking mechanism is basically the same throughout the Curculionoidea, except that it is radically modified in Attelabidae and Rhynchitidae in an obvious specialization (Wood 1978, and unpublished drawings). A minor departure occurs in Scolytidae (Corthylini) (Wood 1978).

Visible abdominal sterna 1 and 2 are entirely free in all primitive genera of Platypodidae but are weakly connate in the higher Platypodidae, all Scolytidae, and in most higher Curculionoidea.

The larvae present an enigma. Except in the most primitive genera, the frons and clypeus are usually fused in Platypodidae (Browne 1972), as in Nemonychidae (Crowson 1967), thus making them easily distinguishable from those of Scolytidae. However, characters have not yet been found that distinguish some Scolytidae from some Curculionidae (Viedma 1963). The difficulty may come more from reduction and simplification to accommodate small size than from real differences. Browne (1972) reported urogomphi-like structures in two species of Platypodidae; if correct, this is the only known occurrence of these structures in the Curculionoidea.

DISCUSSION

Scolytidae and Platypodidae as Families

A position within the Curculionoidea is universally accepted for Platypodidae and Scolytidae, except for Schedl (1939), who gave them superfamily status without explanation. For more than a century, it was traditional to list Platypodidae and Scolyltidae as separate families next to Curculionidae until Crowson (1967:164) combined both families with Curculionidae, primarily on the basis of the absence of convenient larval characters that could separate them from that family. How-

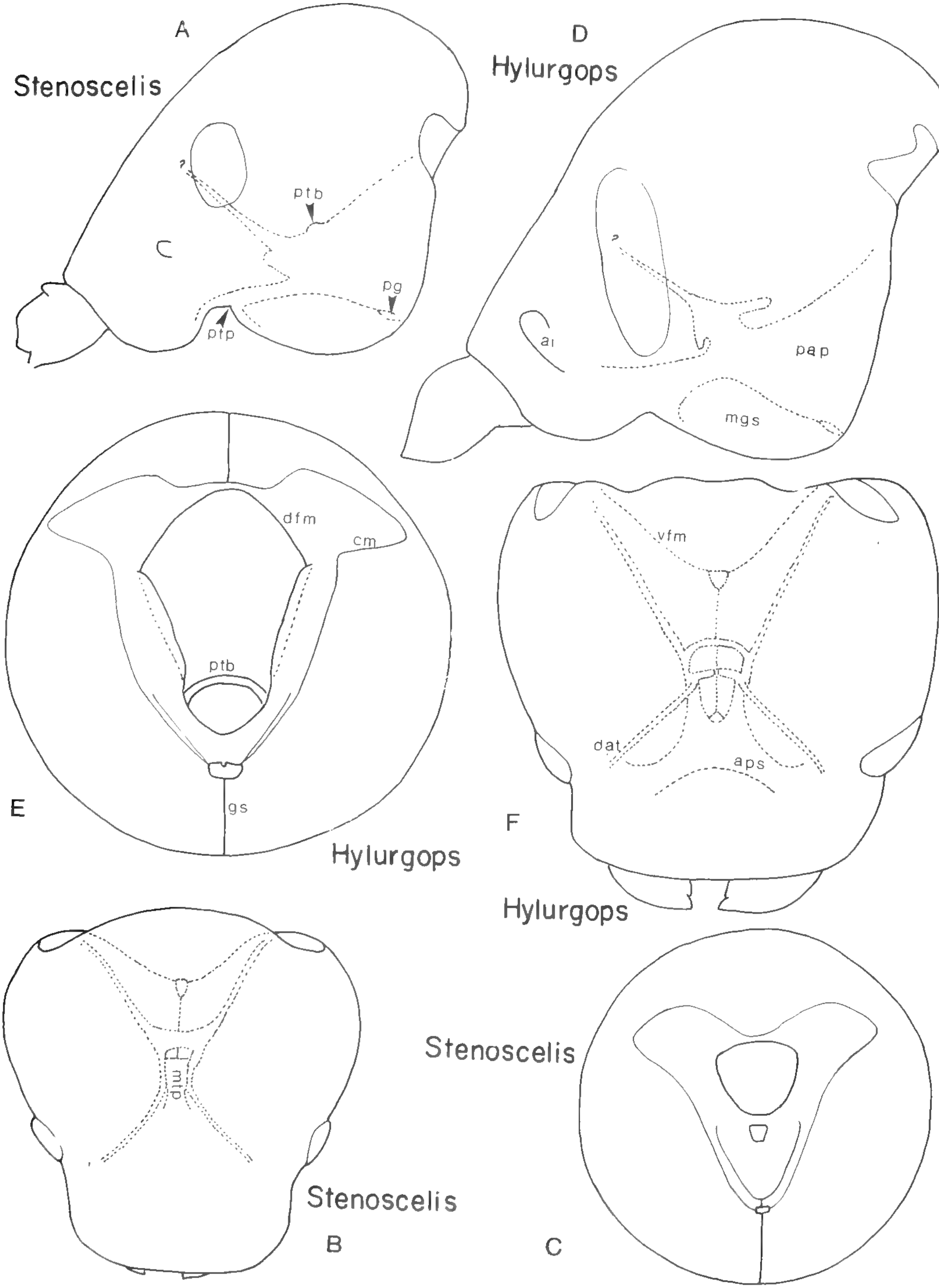


Fig. 5 A–F. Head structure of Curculionidae (*Stenoscelis*, *Rhyncolus*) and Scolytidae (*Hylurgops*, *Ips*): *Stenoscelis brevis* (Boh.) (Curculionidae), A, lateral, B, dorsal, and C, caudal, with internal tentorial and associated structure indicated by broken lines; *Hylurgops rugipennis* (Mannerheim), D, lateral, E, posterior, F, dorsal, internal structure as above.

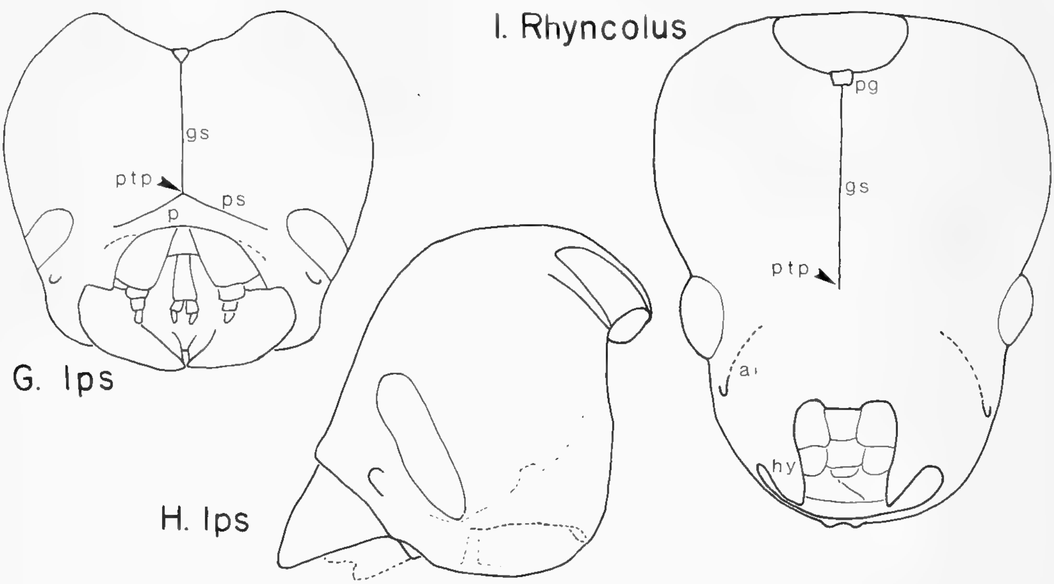


Fig. 5 G–I. *Ips woodi* Thatcher, G, ventral, H, lateral; *Rhyncolus knowltoni* Thatcher (Curculionidae), I, ventral. Abbreviations: ai = antennal insertion; aps = apodeme formed internally by pregular suture; dat = dorsal arm of tentorium; dfm = dorsal margin of foramen magnum; e = cervical membrane attachment; gs = gular suture; mgs = internal apodeme formed by the median gular suture; mtp = median tentorial pillar that invaginates from the combined posterior tentorial pits; p – pregula; pap = paired apodemal plates that branch dorsad from mgs and bears the tentorial apparatus at its anterior extremities; pg = postgula; ps = pregular sutures; ptb = posterior tentorial bridge; ptp = posterior tentorial pit.

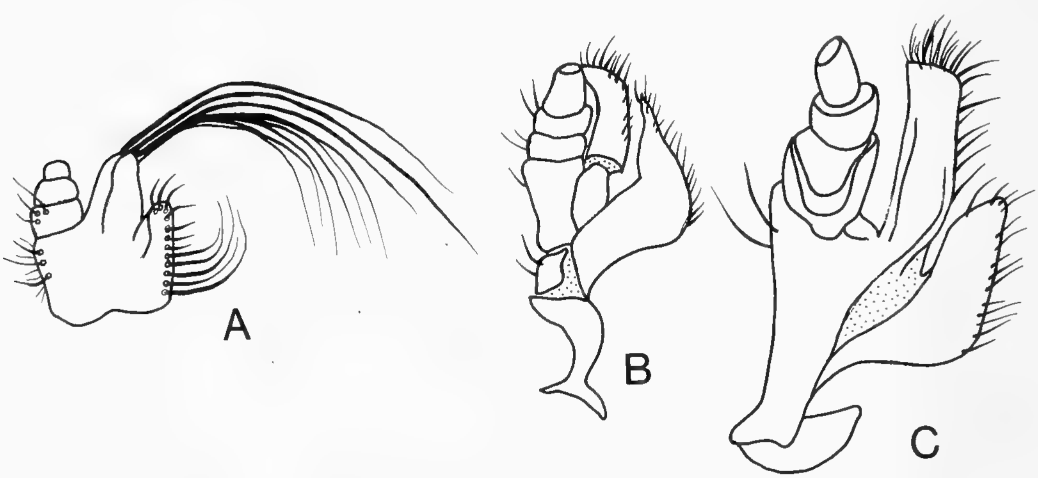


Fig. 6. Maxilla of Platypodidae: *Periommatus bispinus* Strohmeyer (left); *Chaetastus tuberculatus* (Chapuis) (center); and *Tesserocerus insignis* (Saunders) (right). Note the separate galea and lacinea. Re-drawn from Strohmeyer (1914: pl. 1).

ever, following more than 30 years of study of the comparative anatomy of the Curculionoidea, I find that position untenable and suggest that the relationship of Platypodidae and Scolytidae to Curculionidae is remote, at best, and warrants much closer examination. Platypodidae and Scolytidae universally share with one another: (1) well-developed pregular sutures that are reinforced internally by massive apodemal inflections of the entire cuticle,

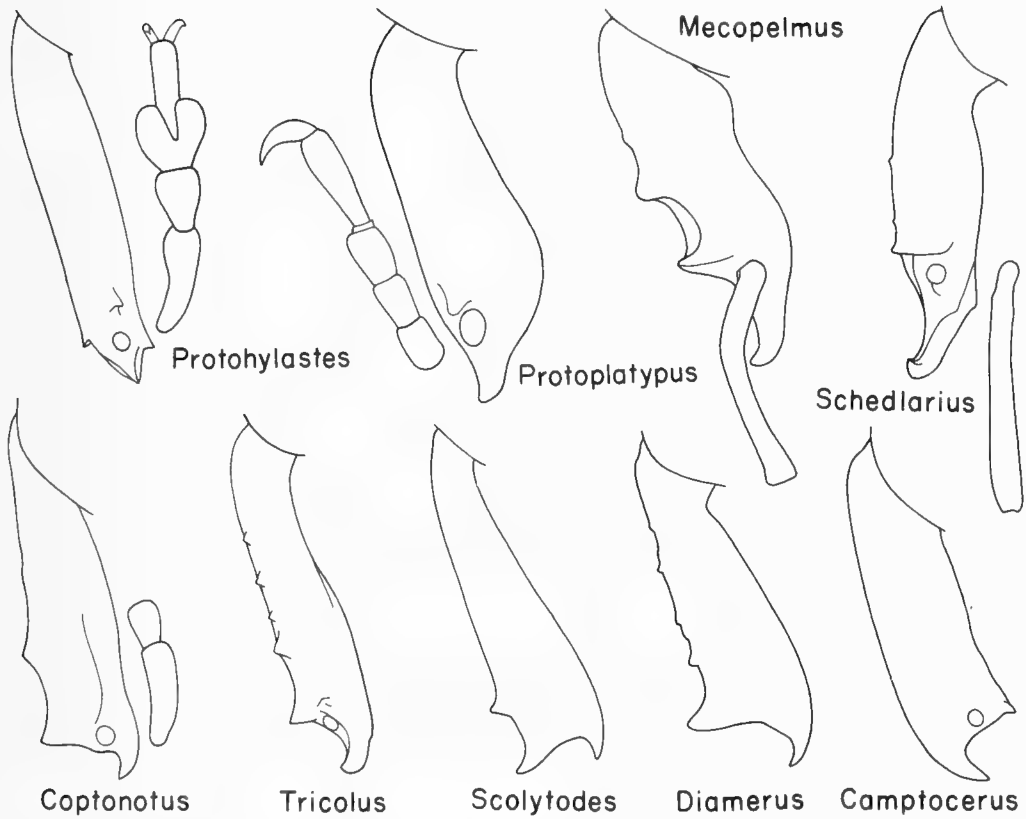


Fig. 7. Posterior face of prothoracic tibia: *Protohylastes annosus* Wood (Coptonotinae), *Protoplatypus vetulus* Wood (Coptonotinae), *Mecopelmus zeteki* Blackman (Coptonotinae), *Schedlarius mexicanus* (Dugès) (Coptonotinae), *Coptonotus cyclops* Chapuis (Coptonotini), *Tricolus peltatus* Wood (Scolytinae, Corthylini), *Scolytodes* sp. (Scolytinae, Ctenophorini), *Diamerus impar* Chapuis (Hylesininae, Deamerini), *Camptocerus auricomus* Blandford (Scolytinae, Scolytini). Each drawing made at different scale so as to reproduce at a uniform size.

extending from the posterior tentorial pit (at the anterior end of the median gular suture) to or near the anterior tentorial pit adjacent to the anterior articulation of the mandible (Figs. 4-5), and (2) a primitive mandible that is articulated and functions (about as in Anthribidae and Nemonychidae) in a manner entirely different from that of higher curculionoids (Fig. 8).

In view of these universally present primitive characters, relict retention of other ancestral features in one or more genera of these two families takes on added significance. For example: (1) The platypodid genus *Austroplatypus* clearly has a 4-segmented maxillary palpus (Browne 1971a) (known elsewhere only in Anthribidae, Nemonychidae, Attelabidae, and some Rhynchitidae). (2) The platypodid tribe Tesserocerini has the maxilla clearly divided into separate lacinear and galear elements (Fig. 6); elsewhere in the Curculionoidea this character is shared by the same four families (cited here in No. 1). (3) An adult labrum within the Curculionoidea occurs only in Anthribidae and Nemonychidae; however, an epistomal lobe resembling a fused labrum is widely represented among primitive Scolytidae (Fig. 1) and is usually present in Platypodidae (in *Tesserocerus* and *Chaetastus*, Fig. 2, it is even separated from the epistoma by a suture). (4) A complete gula, with two gular sutures continuous with the pregular sutures, is present in at least five *Gnathotrupes* (Scolytidae) species (Wood 1973a), and the pregula is greatly prolonged in eight other species of this genus; the pregula is greatly enlarged and the median gular suture is short to very short in most Platypodidae (Fig. 4). (5) In most Platypodidae and many scolytid Hylesinini, Scolytini, Mi-

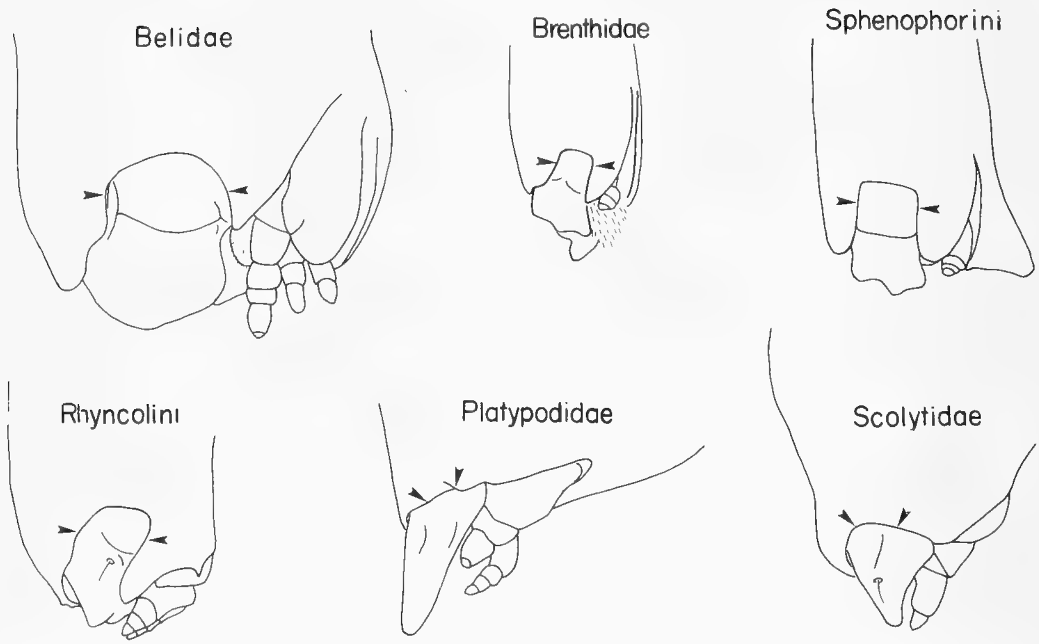


Fig. 8. Lateral aspect of apex of rostrum of a representative of: Belidae, Brenthidae, Sphenophorini (Curculionidae), Rhyncolini (Curculionidae), Platypodidae, and Scolytidae. The arrows mark the approximate position of the concealed anterior and posterior articulations of the mandible.

cracini, etc., the scape is very short, little if any longer than the pedicel and definitely not geniculate, and in other groups (some *Phloeotribus*, some Micracini, etc.) the club is poorly formed; very little imagination is needed to see the possibility of independent origin of the geniculate, clubbed antenna from that of other curculionoids. (6) The costate lateral margins and concave pleura of scolytid Diamerini, Ctenophorini, and some Scolytini occur elsewhere in the Curculionoidea only among the most primitive families. (7) The platypodid-scolytid tibiae totally lack corbels. Their lateral margins bear true spines in Platypodidae and some primitive Scolytidae. These are replaced in all higher Scolytidae by socketed denticles of setal origin that occur nowhere else in the Curculionoidea (Wood 1978); true spines also occur in some Histeridae, Bostrichidae, and other families that frequent the tunnels of woodboring insects. (8) Although the literature states that visible abdominal sterna 1 and 2 are connate in all Platypodidae, this is not true. These segments are entirely free in all primitive genera; they are weakly connate in the higher Platypodidae and in all Scolytidae. An independent origin of this feature is probable. (9) The platypodid-scolytid body habitus most certainly is not of the Curculionidae type, although there is superficial resemblance to it in the Hylastini.

Family Scolytidae

In the early stages of this study, I was thoroughly convinced that Platypodidae could be no more than a well-marked, primitive subfamily of Scolytidae. In view of the often infinitesimally minute features used to characterize other families, that position must be reexamined. Although most characters are shared by some members of each group, a sharp demarkation remains. For example, the male spiculum gastrale is undeveloped in Platypodidae, but it is well-developed in Scolytidae (Wood 1982); tarsal segment 1 is greatly elongated in all Platypodidae (Fig. 9), except for *Protoplatypus* and *Scolytotarsus*, but it is intermediate in *Protohylastes* and *Coptonotus* (These four genera contain a total of five rare, tropical species). The shape and structure of the head, eye, antenna, pronotum, scutellum, elytra, and tibiae are almost equally distinctive. Details of platypodid be-

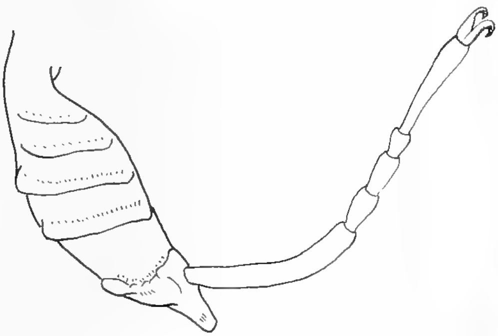


Fig. 9. Posterior aspect of protibia of *Platypus parallelus* (Fabricius) (Platypodidae).

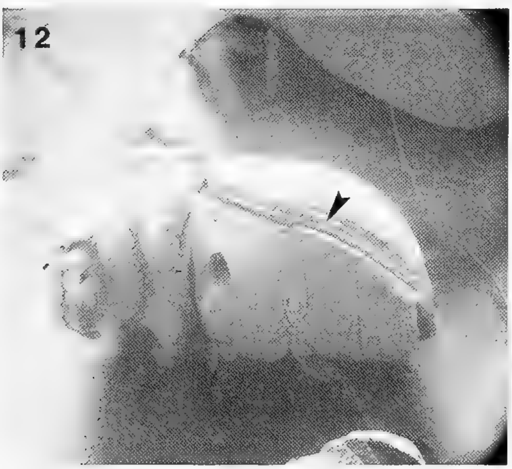
havior are too poorly known to add conclusive supporting evidence. The higher Platypodidae appear to have been the most primitive segment of this phyletic line to take up the woodboring ambrosial habit, which drastically affected their morphology; this habit appears to have arisen independently in at least eight tribes of Scolytidae (Hyorrhynchini, Phloeosinini, Scolytini, Scolytoplatypodini, Xyloterini, Xyleborini, Cryphalini, Corthylini) (Wood 1982).

The Platypodidae universally lack socketed tibial denticles (derived from setae) (Figs. 7, 9); these structures are present in all higher groups of Scolytidae (Fig. 10) but are lacking in at least some genera of several primitive tribes. In all primitive genera of Platypodidae visible abdominal segments (sterna) 1 and 2 are free; in the higher Platypodidae and in all Scolytidae they are weakly connate. The posterior half of elytral interstriae 10 is universally present in Platypodidae; it is present in primitive members of most tribes of Scolytidae (Fig. 12), but it is lost in the higher members of almost all tribes (Fig. 11). The apical protibial mucro of Platypodidae appears to have been derived from the middle apical spine of a tibia resembling that of *Protohylastes* (Wood 1973a); it appears to have been derived from the inner (mesal) spine in Scolytidae (Fig. 7). In larval Platypodidae (except *Protoplatypus* and *Schedlarius*) the clypeus is fused to the frons (Browne 1972); in Scolytidae it is a separate sclerite. The list could go on, but the above should indicate a close relationship between the two families and the limited overlap of many characters.

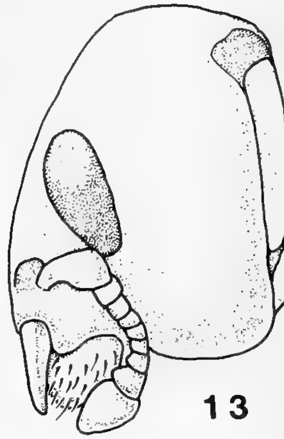
Fig. 10. Lateral margin near apex of protibia of *Polygraphus rufipennis* (Kirby). Note the socketed denticles.

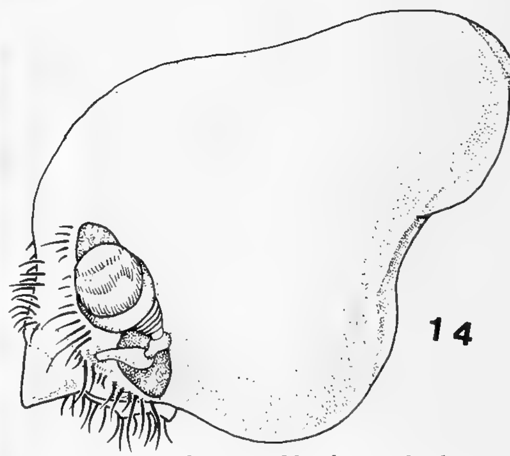
Subfamilies and Tribes

A review of characters usable in classification of the higher categories of Scolytidae was presented by Wood (1978). Several trends were reported in that study: (1) the primitive head is more or less truncate on its posterior face, the dorsomedian area is progressively prolonged caudad in specialized groups (Figs. 13-14, and Wood 1982:Fig. 14); (2) the primitive frons is convex in both sexes (in the higher Hylesininae the male frons is variously impressed and the female frons is usually convex); the reverse is usually found in the Scolytinae; (3) the primitive eye is oval, entire, and finely faceted; specializations include elongation, emargination (including complete division into two parts) (Fig. 15), and enlargement of facets (apparently correlated with nocturnal flight habits); (4) the antennal scape primitively may have been short, little longer than the pedicel; it is elongate or triangular in most groups; (5) the antennal funicle primitively contains seven segments, and there is a more or less orderly reduction to a minimum of one segment as specialization increases; (6) the antennal club varies from almost nonexistent (three movable segments no longer than those of the funicle in primitive *Phloeotribus*) to a simple cone-shaped structure with transverse sutures to large and



Figs. 11-12. Lateral aspect of Scolytidae: 11, above, interstriae 10 unites with interstriae 9 before the level of the hind coxae in *Eupagiocerus dentipes* Blandford; 12, below, interstriae 10 continues to near apex of the elytra in *Scolytodes plumeriae* Wood.





Figs. 13-14. Lateral aspect of head in Scolytidae: 13, *Hylastes nigrinus* Mannerheim, with the posterior face approximately truncate; 14, *Xylosandrus retusus* (Eichhoff), with the occipital area greatly extended.

strongly flattened or obliquely truncate, with or without sutures; it is probably the most variable major structure found throughout the family; (7) the prothorax may have (a) the coxae widely separated in primitive groups to fully contiguous in specialized ones; (b) the pleuron concave, with the lateral margins acutely costate in primitive genera (Figs. 11-12), to convex, with the lateral margin unmarked in specialized genera; (c) the pronotum longitudinally straight in dorsal profile and unarmed by crenulations in primitive groups to strongly arched and armed by crenulations or asperities in specialized ones; (8) the basal margins of the elytra tend to be costate primitively, with the Hylesininae becoming procurved and crenulate (Fig. 16), the Scolytinae transversely straight and longitudinally rounded (Fig. 17); (9) several complex changes occur in the meso- and metathorax that will be discussed below; (10) the male tergum 8 is visible and pubescent in most groups (Fig. 22), but it is telescoped beneath 7 and without pubescence in Carphodicticini, Ipini, Dryocoetini, Xyloterini, and Xyleborini; (11) the venter of the abdomen has (a) segments 3 and 4 (visible segments 1 and 2) free in all primitive Platypodidae but weakly connate in the higher Platypodidae and all Scolytidae and (b) limited specialized groups in which specialized features are very impor-

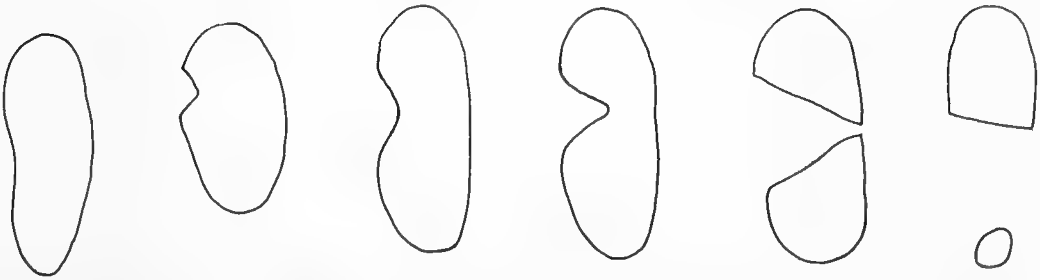
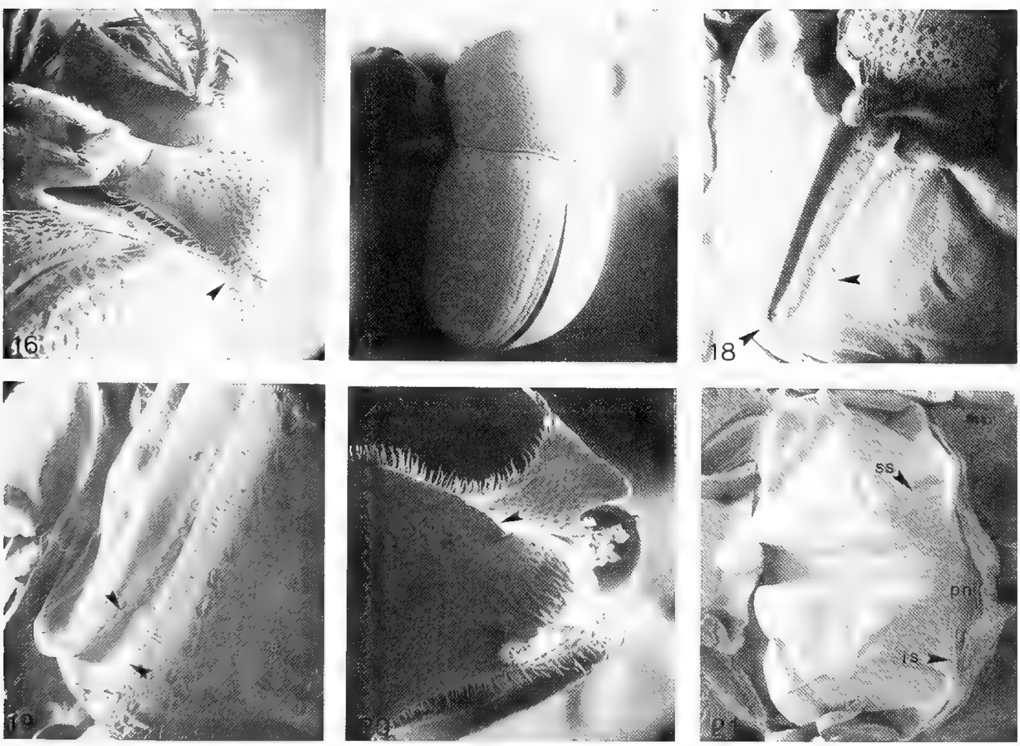


Fig. 15. Variations in eye shape (left to right). shallowly sinuate (*Hylesinus crenatus* Fabricius); narrowly and shallowly emarginate (*Ernoporicus caucasicus* Lindemann); strongly sinuate or broadly, shallowly emarginate (*Phloeosinus bicolor* Brulle); deeply emarginate (*Phloeosinus thujae* Perris); completely, equally divided (*Polygraphus poligraphus* Linnaeus); and completely, unequally divided (*Sphaerotrypes globosus* Blandford).



Figs. 16-21. Thoracic structure of Scolytidae: 16, elevated crenulations (arrow) on procurved basal margins of elytra of *Phloeotribus setulosus* Eichhoff; 17, weakly subcostate basal margins of elytra in *Scolytodes plumeriae* Wood; 18, metatergum of *Hylastes nigrinus* Mannerheim, arrows mark intersegmental line (left) and scutoscutellar suture (right); 19, metapleuron of *Hylastes nigrinus* Mannerheim, upper arrow marks pleural suture, lower arrow marks anterior end of groove that receives costal margin of elytron; 20, ventrolateral aspect of prothorax, arrow marks acutely elevated precoxal ridge (or costa); 21, metatergum of *Eupagiocerus dentipes* Blandford, pn = postnotum, is = fused intersegmental line, ss = scutoscutellar suture (compare to Fig. 18).

tant (*Scolytus*, *Scolytomimus*, etc.); and (12) the tibiae are unusually variable and require special treatment below.

Most of the above character states are utilized in the following key to subfamilies and tribes to indicate phyletic trends in the family, subfamily or tribe in which they are involved. However, two of them are sufficiently complicated and important that elaboration is appropriate. These occur on the metathorax and the tibiae.

Three primary characters of the metathorax show important features that exhibit phyletic

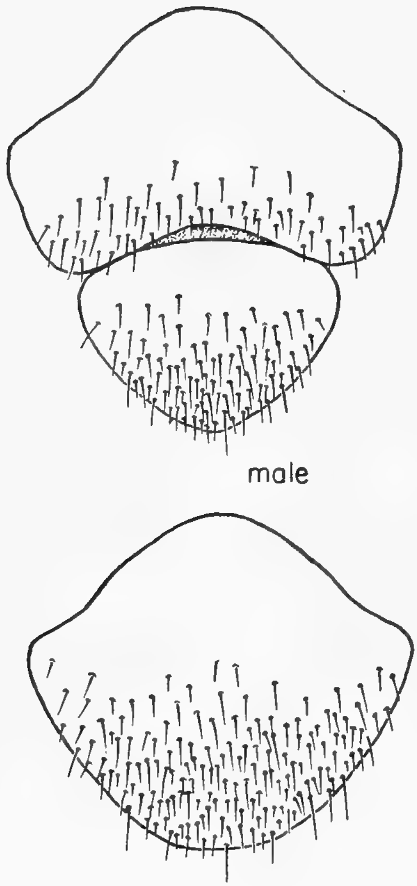


Fig. 22. Abdominal terga of *Cryphalus ruficollis* Hopkins: male, with segments 7 and 8 visible; female, with segment 7 visible (segment 8 is reduced in size, telescoped beneath 7, and hidden from view).

trends. First, in Curculionoidea generally, including Platypodidae and primitive Scolytidae, the pleural suture follows a zigzag course from the pleural wing process ventrad to the point where the costal margin of the elytron touches the body. It then turns abruptly caudad to a point just before reaching the posterior limits of the segment, where it turns mesad and continues to the pleural coxal process. On the metepisternum at the anterior or first angle (below the pleural wing process) a carina or small, flattened spine is present that fits into a small groove on the inner (costal) margin of the elytron just behind the humeral angle. This character state within Scolytidae is best seen in the Hylastini (Fig. 23, parts 43-44) and in some Hylesinini. The trend is for the suture to progressively straighten out whereas the metepisternal spine remains stationary but becomes more remote in position from the changing suture (Fig. 23, part 42). The matching groove on the elytron moves somewhat dorsad and caudad, suggesting that the costal margin of the elytron extends farther ventrad than primitively. In Cryphalini the metepisternal spine is considerably reduced in size, and its function in locking the elytra in closed position is partly assumed by a new diagonal groove on the metepisternum (Fig. 31). In Corthyulini, the spine is entirely lost and the groove is enlarged and extends to a more ventral position (Figs. 23, part 47, and 32). The result is that the closed elytron in this tribe now covers all but a small anterior portion of the metepisternum.

A second significant feature of the metathorax involves progressive changes in position of the scutoscutellar suture. In Curculionoidea generally, Platypodidae, and primitive Scolytidae (Hylastini and Hylesinini are examples), this suture reaches the margin of the scutellar groove near the anterior limits of the groove and continues parallel to and very near its lateral crest for about two-thirds of the length of the groove, then the suture curves abruptly laterad to follow its usual course to the posterior margin of the segment (Fig. 23, part 43). In more advanced tribes this suture progressively straightens out, meeting the marginal crest of the groove only briefly, if at all (Fig. 23, part 41).

The third significant metathoracic feature that is usable in phylogeny occurs only in the Hylesininae. A significant feature of insect flight is the intersegmental line between the metathorax and its postnotum (derived primitively from the anterior portion of the first abdominal segment but functionally part of the thorax), which must flex with each stroke of the metathoracic wings. This suture is present in all insects, including Platypodidae, Scolytinae, and primitive Hylesininae (Fig. 23, parts 43, 45). In the more advanced Hylesininae, the median two-thirds of this intersegmental line is lost by complete fusion of the postnotum to the metathorax (Fig. 23, part 41). This fusion is progressive, leaving a weak suture primitively, but it is totally obliterated in advanced groups of this subfamily.

The tibiae exhibit remarkable variation in constant, conservative patterns that are valu-

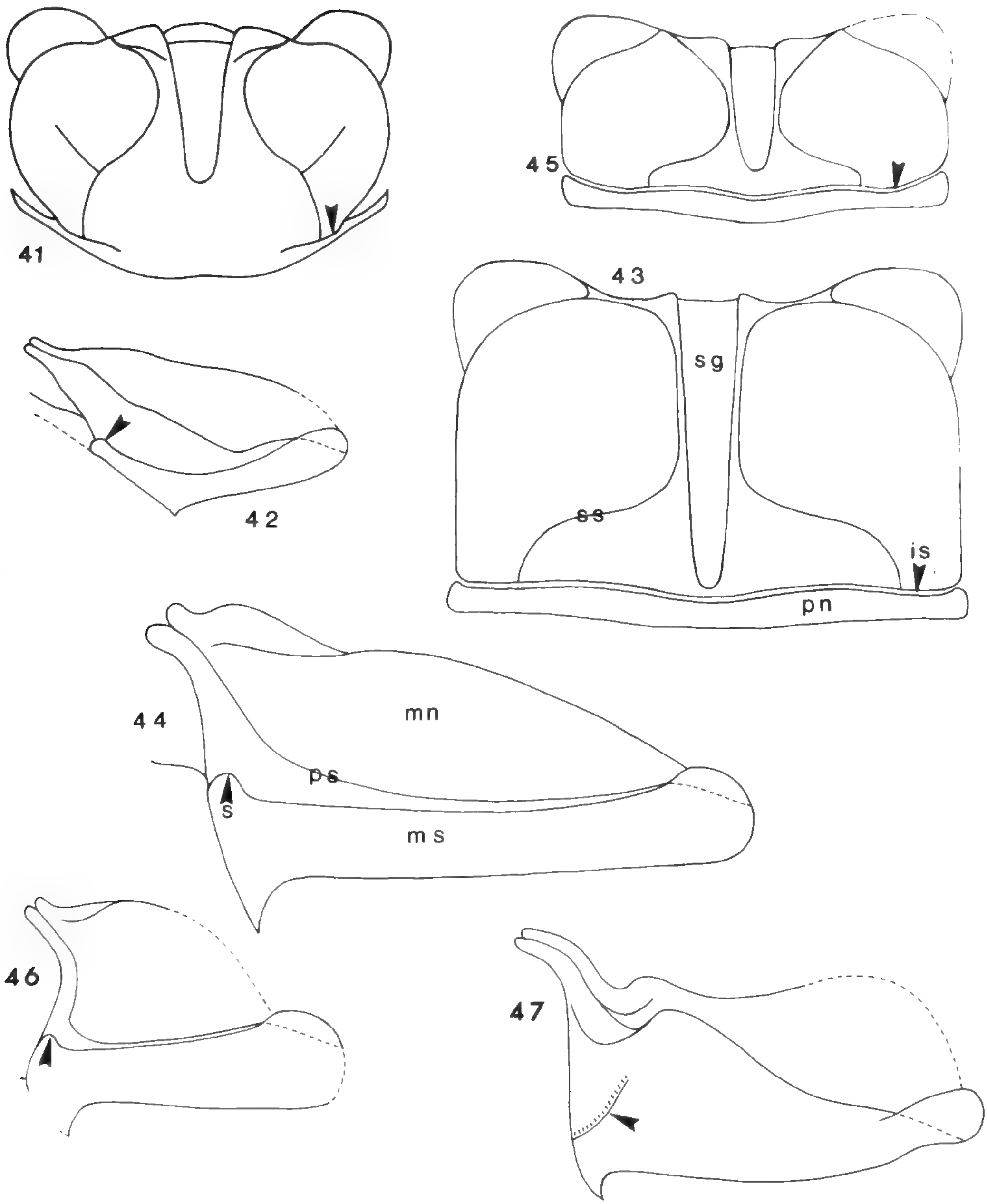


Fig. 23. Diagrams of terga and pleura of Scolytidae: 41, metatergum and 42, pleuron of *Chramesus hickoriae* LeConte, arrow points to remnant of intersegmental suture in 41, to metepisternal spine in 42; 43, metatergum and 44, pleuron of *Hylastes nigrinus* Mannerheim, arrows as above; 45, metatergum and 46, pleuron of *Cnemonyx panamensis* (Blandford), arrows as above; 47, pleuron of *Pityophthorus crotonis* Wood, metepisternal spine is lost and is replaced by a small groove (arrow). Abbreviations: is = intersegmental suture, mn = metepimeron, ms = metepisternum, pn = postnotum, ps = pleural suture, s = metepisternal spine (part of locking mechanism for elytra), sg = scutellar groove, ss = scutoscutellar suture.

able in following trends in phylogeny. Apparently, the primitive model from which the tibiae of Platypodidae and Scolytidae were derived resembles that of *Protohylastes* (Fig. 7). The protibia of *Protohylastes* is slender, with three rather small spines at the apex and

a very minute spine on the posterior face immediately basad from the tarsal insertion. Comparative studies (Wood 1973, 1978) suggest that the mesal (inner) apical spine became the apical spine in Scolytidae and that the middle spine became the apical spine in Platypodidae (Figs. 7, 9). This middle spine in Scolytidae is bent laterad and is a major, identifiable element that projects beyond the level of the tarsal insertion in one or more members of several tribes (Hyorrhynchini, Diamerini, Bothrosternini, Phloeotribini, Phloeosinini, Hypoborini, Polygraphini, Scolytini, Ctenophorini, Scolytoplatypodini). All tibial spines in Platypodidae (Fig. 9), Hyorrhynchini, Scolytini (Fig. 7), and, apparently, Ctenophorini (Fig. 7) are true spines. In all higher Scolytidae these spines are either intermixed with or replaced by socketed denticles of setal origin (Fig. 10). The patterns of possession and replacement within the family suggest that socketed denticles had an early monophyletic origin within the Scolytidae, with differential survival of this character in the posterity, and do not suggest polyphyletic origins.

Many other characters that are not mentioned above are useful in classification and phylogeny in more limited groups. Several of these are employed in the keys.

Conclusions

As stated above, the traditional place of Scolytidae in classification has been as a family next to the Curculionidae. However, as Curculionidae became fragmented into several families, the position of Scolytidae within the Curculionoidea changed. Schedl (1939c) made a separate superfamily to contain Platypodidae and Scolytidae. Crowson (1967:164) reduced both to the rank of subfamily within Curculionidae.

In reviewing this topic, our first point has been to establish that Platypodidae and Scolytidae are closely related to each other and are derived from the same parental stock. Evidence for this, as stated above, comes from the following: (1) Pregular sutures that extend from the anterior tentorial pit (adjacent to the anterior articulation of the mandible) to meet the anterior end of the median gular suture occur only in these two groups. These sutures are reinforced internally by massive apodemes. Remnants of pregular sutures found in females of two species of Belidae extend from the anterior tentorial pit toward the antennal insertion and never converge or approach the gular suture (or sutures). (2) In these two families, the mandibles come to an apical point and have the cutting edge mesal as in Nemonychidae; furthermore, the articulating condyles are comparatively close together, with the posterior one more nearly lateral in position, and the hypostomal area behind the posterior condyle is minimal in size to almost nonexistent. In most Curculionoidea, except for these two families and Nemonychidae and Anthribidae, the basal half of the mandible forms a horizontal cylinder that rotates on the two condyles, and the cutting edge of the mandible is apical; the posterior condyle is posterior in position and is supported by an enlarged hypostomal area. (3) The subcortical habit in which mated pairs enter vital host tissues to oviposit is shared by Platypodidae, Scolytidae, and some Cossoninae (Curculionidae); however, the mode of excavation and several structural features (gular area, tentorium, mandible, etc.) indicate that the latter group exhibits an evolutionary parallelism, not a fundamental relationship. (4) Six genera (*Protohylastes*, *Coptonotus*, *Scolytotarsus*, *Protoplatypus*, *Mecopelmus*, *Schedlarius*) are structurally and biologically intermediate between the Platypodidae and Scolytidae and could be placed in either family. The characters, reviewed in this paragraph, with primary stress placed upon true pregular sutures, indicate a fundamental close relationship between Platypodidae and Scolytidae that is not shared with other groups.

A second point of significance has to do with the position of Platypodidae and Scolytidae within the Curculionoidea. Their traditional position in classification has been next to the Curculionidae; however, close examination suggests that such a placement is based on superficial resemblance, not on fundamental structure. As indicated above, pregular sutures are shared, in part, only with females of two species of Belidae, and the mandibular-hypostomal structure is shared only with Anthribidae and Nemonychidae. These indications suggest a relationship of Platypodidae and Scolytidae to the segment of Curculionoidea having two gular sutures, rather than

one. However, close inspection of Belidae discloses at least three genera with only one median gular suture and an elongated postgula, and an entire segment of Oxycorynidae (*Rhopalotria*) with one gular suture and a postgula of variable size. Furthermore, one genus of Scolytidae (*Gnathotrupes*) contains at least five species with a complete gula connecting pregular and postgular elements, and at least eight more in which the connection is almost complete. In many Platypodidae, the pregula is enlarged and is scarcely separated from the postgula. Because such a situation does not occur elsewhere among those curculionoids having one gular suture, wisdom suggests that a search be continued for additional clues to phyletic relationships.

A movable labrum occurs among curculionoids only in Anthribidae and Nemonychidae. Remnants of a labrum are found in many primitive Scolytidae (particularly Hylesininae), and a fused labrum, complete with a transverse suture, occurs in Platypodidae (especially Tesserocerini). I am unaware of similar remnants in other curculionoid families.

A 4-segmented maxillary palpus occurs in *Australoplatypus* (Browne 1971a:49), a feature restricted to only the most primitive curculionoids (see family key below).

A lacinia separate from the galea is characteristic of all Tesserocerini (Platypodidae); this is another feature that is restricted to the most primitive curculionoids (see family key below).

The antenna has been used extensively in the classification of curculionoid families, particularly character states of orthocerous vs. geniculate, apex filiform vs. clubbed (or capitate), etc. In no curculionoid are segments 1 and 2 without some degree of enlargement; furthermore, in many of those traditionally referred to as geniculate, the scape is not longer than it is in some Anthribidae. In a large segment of Platypodidae and many Scolytidae, the scape is short, little if any longer than the pedicel, and often it is broadly triangular in shape. In virtually all curculionoids (except most Anthribidae), the three apical segments of the antenna are at least slightly enlarged; although the literature generally states otherwise, a few Anthribidae have an abruptly enlarged club. In the genus *Phloeotribus* (Scolytidae), the club is usually sublamellate, with the three segments freely movable upon one another (Fig. 16). In primitive members of this genus (*acaciae*, *rhododactylus*, etc.) the three segments are no longer or wider than are the funicular segments and are as movable. I see no possibility that the *Phloeotribus* antenna could have been derived from a solid club of the type found in most other Scolytidae. Since this is the only deviant character found in this genus, could it not be a relict reminder that the scolytid club was derived on an independent, parallel line from a common ancestor, and not from other curculionoid groups having clubbed antennae?

Much has been said and written of the similarity of the tibiae between *Scolytus* (Scolytidae) and many Cossoninae (Curculionidae) in curculionoid family classifications. However, it has never been pointed out that similar tibiae occur in Histeridae, Brenthidae, and other coleopterous families containing groups with a long history of subcortical existence. Within the Scolytidae, the *Scolytus* tibia is unique and apparently does not represent a truly primitive condition. The truly primitive character state of the tibia on this phyletic line occurs in *Protohylastes*, with Platypodidae and Scolytidae derived along separate phyletic lines from the basic structure.

Larval characters, thus far, have not been very helpful in answering questions about scolytid phylogeny. In fact, reliable means have not yet been found for separating all Scolytidae from all Curculionidae (Viedma 1963, Lekander 1968). Whether this is due to the absence of characters or to the lack of diligence in the search for characters among groups not found in Europe needs to be answered. Primitive larval Platypodidae have the frontal sutures extending to the articulating membrane of the mandibles, a fact not previously noted. Browne (1972) suggested that structures found on two platypodid larvae could be relicts of urogomphi. If so, this is the only evidence of the existence of urogomphi in the Curculionoidea. Larval Scolytidae and Platypodidae are easily separated from each another by the separate (Scolytidae) or fused clypeus and frons (Platypodidae). It is of interest that this same character separates larval Nemonychidae and Anthribidae (see family key below).

Lower Jurassic curculionoids with a long rostrum have been referred to the Curculionidae by Crowson (1983), although they bear a very strong resemblance to Belidae or, perhaps, Eobelidae. Arnoldi (1977) named the extinct family Eobelidae from 14 species that were placed in 7 tribes in 4 subfamilies, taken from Upper Jurassic deposits of South Kazakhstan (Karastan) in the USSR. In this family the head is similar to modern Belidae except that it is more broadly oval and the rostrum is shorter, as in some modern male Brenthidae. The mandibles are large, with a single apical point and a mesal cutting edge as in modern Nemonychidae. The antennae attach either to the middle or near the apex of the rostrum and are orthocerous, with the three apical segments slightly enlarged but not forming a definite club. Arnoldi did not mention gular sutures or a labrum. The body resembled modern Belidae except that the lateral margins of the prothorax were acutely elevated as in modern Oxycorinidae and the elytra were much less strongly sclerotized than in modern Belidae.

From the above, two fundamental conclusions emerge. First, the Platypodidae and Scolytidae are very closely related to one another and, in fact, they intergrade to a limited extent. At the same time, these two families are quite distantly related to other families in this superfamily. Second, in spite of the apparent absence of larval characters, there are enough discordant adult characters to conclusively demonstrate that the Platypodidae-Scolytidae, as one unit, do not belong to and probably are not even closely allied to Curculionidae. It is my contention that their pregular sutures (and accompanying internal apodemes) prevented elongation of the rostrum and forced them into an entirely different mode of existence from other curculionoids (parent adults had to bore into vital host tissues to oviposit because they had no rostrum and, consequently, could not follow the curculionid habit of using the rostrum to form oviposition pits). They could have been derived in the Jurassic from a short-rostrumed Eobelidae-like ancestor that had fully formed pregular sutures. Belidae and related families, and all other curculionoids having one gular suture, branched off later or from other segments of Eobelidae or its derivatives. Rostrum length among Jurassic curculionoids was diverse, varying from short and broad (Arnoldi 1977) to long and slender (Crowson 1983). The presence of obvious, sophisticated scolytid tunnels in Lower and Middle Cretaceous conifer bark suggests that the Platypodidae-Scolytidae phyletic line had its origin at least in Upper or Middle Jurassic. The exact phyletic positions of known Jurassic and Cretaceous "curculionid" fossils are difficult to determine, because details of labrum, mandibles, gular sutures, etc., are not sufficiently well preserved to permit analysis. I seriously doubt that any true Curculionidae existed prior to the Cretaceous.

Habits and Classification

Although the Platypodidae are established above as a family, separate from Scolytidae, they are significant because they represent the first major paraphyletic branch from the platypodid-scolytid line of specialization. Their adoption of the xylomycetophagous habit appears to have accelerated their structural and biological deviation. Only the intermediate genera *Protoplatypus*, *Mecopelmus*, and *Schedlarius* lack the ambrosial habit (*Protohylastes*, *Scolytotarsus*, and *Coptonotus* are unknown biologically). *Schedlarius* (monogamous) and *Protoplatypus* (polygynous) place their eggs in sealed niches; all other known platypodids are monogamous and distribute the eggs loosely in the parental galleries or carry them on the female frons. *Mecopelmus* makes a cave-type nuptial chamber (without oviposition galleries) in the cambium region of its host and deposits the eggs in clusters therein, and the larvae form independent mines in the cambium at least for the latter part of their development. *Protoplatypus* forms stellate or radiate tunnels, with a central nuptial chamber in the cambium region, and the eggs are placed in regular, alternate, sealed niches along the linear egg galleries; the larvae form independent mines throughout their development. *Schedlarius* is xylophagous (Wood 1957a), places its eggs in randomly organized niches that are sealed with frass, and the larvae form long, independent mines that wander aimlessly through the wood. An obvious association with fungi is apparent in the vicinity of adult and larval activity, although no mycelial growth in the

mines could be seen at magnification of 20X. The habits mentioned in this paragraph also form the basis of habits for the more diverse Scolytidae.

In my review of characters usable in distinguishing subfamilies of Scolytidae (Wood 1978), only one significant character gap was found that was supported by numerous features. These characters are summarized in the key to tribes below. The presence or absence of pronotal asperities, the ambrosial habit, and several features used traditionally by past workers to separate multiple subfamilies of Scolytidae either have no value in characterizing subfamilies or have no value in phylogeny. For these reasons, only two subfamilies were recognized. Because the Hylesininae are structurally and biologically less diverse and their specializations more conservative, they are treated here as more primitive than the Scolytinae.

Tribes of Hylesininae

In general, the Hylesininae are phloeophagous. Exceptions include the twig- or small-branch (pith)-boring mycetophagous Hyorrhynchini (all three genera), *Bothrosternus* (Bothrosternini), and *Hyleops* (Phloeosinini; last half of larval stage only); xylophagous *Dendrosinus* and three known species of the large genus *Chramesus* (Phloeosinini); the myelophagous *Cnesinus*, *Eupagiocerus*, and *Sternobothrus* (Bothrosternini); and the spermophagous *Pagiocerus* (Bothrosternini) and one species of *Phloeotribus* (Phloeotribini). The usual mating system in this subfamily is monogamy, with the female initiating the new parental gallery. Departures from this system include (a) apparent male haploidy (arrhenotocous parthenogenesis accompanied by consanguineous polygyny) in *Sueus* (Hyorrhynchini); (b) monogamy, with male initiation of parental galleries in some *Phloeosinus* and *Olonthogaster* (Phloeosinini); and (c) heterosanguineous (superficially resembling harem) polygyny in at least two species of New Guinea *Olonthogaster* (Phloeosinini), and in all *Carphoborus* and many *Polygraphus* (Polygraphini).

These basic habits appear to be correlated with (1) a conservative evolutionary departure from the ancestral structure; (2) a more compact (stout) body; (3) the body compaction that appears to have resulted in the development of a row of coarse crenulations on the basal margins of the elytra (their function is evidently to add resistance when a predator attempts to pull from a tunnel the beetle that is blocking the entrance), and (4) the straightening of the pleural suture. The compaction of the body apparently also had an effect upon the mechanism of flight and permitted fusion of postnotum 2 to the metathorax. Although use of these characters requires further study and refinement, a definite trend from the Hylastini-Hylesinini to Phloeosinini is indicated.

There appears to be a gradual transition in characters from the Hylastini to Hylesinini to Tomicini. The Hyorrhynchini and Phrixosomini appear to be relicts of an earlier radiation of primitive stock and are quite unrelated to the other three tribes. The remaining hylesinine tribes have the postnotum partly to entirely fused to the metanotum and fall into three units. The first includes the Old World Diamerini and New World Bothrosternini that probably contain the most primitive species of this subfamily. Their protibial, pronotal, and base of elytral structure is much more primitive than the Hylastini-Hylesinini. Their antennal structure is much more similar to *Coptonotus-Protohylastes* (Platypodidae), although the Hylastini-Hylesinini club is probably more similar to the ancestral structure.

The second tribal unit within the more highly evolved segment of this subfamily includes the Phloeotribini and Phloeosinini. Tibial structure of at least a few representatives of each suggests an ancient origin. Except for the aberrant structure of the antennal club of Phloeotribini, they probably could not be separated from one another at the tribal level. They include species bearing the greatest departures from the primitive forms in the pleural and scutoscutellar suture patterns. The absence of socketed protibial teeth in *Aricerus* and the movable segments in the antennal club suggest that Phloeotrinini is the more primitive of these two tribes.

The Polygraphini and Hypoborini are obviously specialized ancient groups that are unrelated to one another but of uncertain affinity to other groups. The superficial appearance of the body form of *Phloeographus* (Poly-

graphini) suggests a relationship to *Tomicus*, but the protibial structure of *Serrastus* suggests a much more ancient origin of this group. The Hypoborini could be a specialized paraphyletic line that branched from the Phloeosinini.

Tribes of Scolytinae

The tribes of Scolytinae are easily clustered into five major groups on the basis of several anatomical characters. The most primitive, composed of Scolytini, Ctenophorini, and Scolytoplatypodini, share primitive protibial structure without socketed denticles, a 6- or 7-segmented antennal funicle, a head without a caudal extension of the dorsal occipital area, rather widely separated procoxae, etc. This group contains members (*Cnemonyx*, *Scolytodes*) with the greatest structural similarity of all Scolytinae to primitive Platypodidae (*Protoplatypus*, in this instance) and to Hylesininae. In fact, some *Cnemonyx* (*galeritus* and its allies) have coarse crenulations on the basal margins of the elytra; also, *Protohylastes* was thought to be allied to *Pseudohylesinus* (Tomicini) until the legs and antennae were studied. The Ctenophorini habits include phloeophagy, xylophagi, and myelophagy; monogamy and polygyny (heterosanguineous only); egg chambers of the cave, linear and radiate types; and deposition of eggs in loose clusters in parental chambers or in individual niches sealed by frass. The monogamous, xylomycetophagous Scolytoplatypodini appear to be a specialized Old World geographical replacement of the Ctenophorini. The Scolytini are monogamous (except for a few bigynous *Scolytus*) and phloeophagous (except for the xylomycetophagous *Camptocerus*). *Cnemonyx* (Scolytini) and *Scolytodes* (Ctenophorini) could have been derived from a common ancestor. *Pycnarthrum* (Ctenophorini) could easily be placed as a primitive tribe of Hylesininae on both anatomical and biological bases.

The second cluster of tribes within the Scolytinae includes the Micracini and Cactopinini. Advances include a more efficient body form (cylindrical compaction), slightly extended dorsal occipital area of the head, reduction of funicular segments to six (rarely five), universal occurrence of pronotal asperities, common occurrence of xylophagy and bigyny, etc. Xylomycetophagy and males normally associated with more than two females are unknown. Scalelike pronotal and elytral setae are a common occurrence. The evolutionary connection between this group of tribes and the more primitive Scolytini-Ctenophorini-Scolytoplatypodini is remote; however, a connection to the more advanced Xyloctonini-Cryphalini is clearly evident.

The third cluster of tribes within the Scolytinae includes the Carphodicticini, Ipini, Dryocoetini, Crypturgini, Xyloterini, and Xyleborini. In this group, male abdominal tergum 8 is reduced in size and telescoped beneath 7, as in the female. In addition, the procoxae are almost always contiguous, the occipital area of the head attains its greatest prolongation, the obliquely truncate antennal club is developed and exploited, both heterosanguineous and consanguineous polygyny are common, and xylomycetophagy is universal in two tribes. Carphodicticini and some Dryocoetini are obviously very primitive, but their connection to other primitive Scolytinae is remote and not reflected in the modern known fauna. The basal margins of the elytra are elevated and costate in *Dendrodicticus* (Carphodicticini) as in some Hylesininae.

The fourth cluster of tribes within the Scolytinae includes Xyloctonini and Cryphalini. In these tribes the procoxae are entirely contiguous, and the antennal club is flat, with the sutures on the posterior face moderately displaced toward the apex. The small metepisternal spine that functions in locking the elytra in the closed position is reduced and partly replaced by a small groove (Fig. 31). Segmentation of the antennal funicle is reduced, ranging from a maximum of seven to a minimum of three. Monogamy is the general habit, with consanguineous polygyny universal in four genera of Cryphalini (*Cryptocarenus*, *Hypothenemus*, *Trischidias*, *Periocryphalus*). There appears to be a close connection between Micracini and this group of tribes. The elytral locking mechanism also suggests a remote connection between this group and the Corthylini (Figs. 23, 31-32).

The final cluster of tribes includes the Corthylini. The flattened antennal club, with the sutures equal on both sides, the unique elytral locking mechanism, tibiae, eyes, elytra, etc.,

characterize this unique tribe. Phloeophagy is almost universal in the primitive half of the tribe, xylomycetophagy in the advanced half. Both monogamy and heterosanguineous polygyny are common. Consanguineous polygyny apparently occurs in three species of *Araptus*. There may be a remote phylogenetic connection to the Cryphalini.

Geographical Origin of Tribes

For a discussion on this topic to have any semblance of objectivity, certain premises must be established. First, it is assumed that continental drift did occur and, due to that phenomenon, South America and Africa were either connected at their southern ends or were at least close enough to permit faunal exchange by island-hopping until earliest Tertiary. At that time, Australia was close enough to the southern end of South America to permit at least limited faunal exchange. Second, it is assumed that South America was an island during most of the Tertiary. In addition to the assumed connection to Africa in earliest Tertiary, South America was connected to North America in early Tertiary and again in late Tertiary either by a land bridge, as presently exists, or by a series of islands that were close enough to permit faunal exchange. Third, it is assumed that faunal exchange between Africa, Europe, and Asia has been no problem except as it has been affected by climate. Fourth, it is assumed that climate has fluctuated as evidenced by fossil remains of magnolia trees in Alaska and of tropical forests where the Sahara Desert is now located. Finally, it is assumed that scolytid beetles have had habits throughout their history that were essentially as seen at present. That is, groups presently restricted to the tropical forests have always been so restricted, and groups now in more temperate climates have been able to occupy cooler climates for a long time.

In the first column of Table 1 are listed all tribes of Scolytidae presently recognized in the world fauna. From each tribe, those genera were selected that now are restricted to tropical climates. If those genera are now represented in both Africa and South America or if they have a very closely related geographical replacement genus on both continents, but are not found outside the tropics elsewhere, then those tribes were considered to have a pre-Tertiary origin (Table 1, column 2). If the tribe at that time was local in distribution and was represented on only one land mass, it was not included as pre-Tertiary even though it could have been present. A faunal connection from South America to Australia was regarded as early Tertiary, not just pre-Tertiary. It is noted (1) that 6 of 11 tribes of Hylesininae and 7 of 14 tribes of Scolytinae are judged on this basis to be of pre-Tertiary origin, and (2) that the only pre-Tertiary group containing species with the xylomycetophagous habit is Xyleborini. (Hylesinini is excluded, because its only xylomycetophagous genus, *Hyleops*, has not yet fully adopted that habit.) This does not mean that other xylomycetophagous groups were not present, but only that, if they were present, they were local in distribution (on only one land mass) at that time. It is further noted (3) that all tribes judged as pre-Tertiary were phloeophagous except for Xyleborini and part of Micracini. This suggests that xylophagy and xylomycetophagy are of comparatively recent origin.

The significant point is that the family Scolytidae was a well-established, diversified group by the beginning of the Tertiary. The fossil engravings of scolytids in coniferous bark from Upper Cretaceous illustrated by Brongniart (1877) and described from Lower Cretaceous by Blair (1943) are evidence of a much longer family history of the group than is usually recognized. It is probable that the beetles that made those engravings were much more similar to the Ctenophorini or, possibly, *Protoplatypus* than to modern Hylesininae.

PHYLOGENY

As stated above, the Platypodidae-Scolytidae group are members of the Curculionoidea. Within that superfamily, they form a distinctive unit that is characterized by the presence of fully developed pregular sutures. Because the only other known pregular sutures within the Curculionoidea are the apical remnants found in females of two species of Belidae, the possibility of an ancient common ancestor should be examined. Three genera of Belidae and an entire segment of Oxycorynidae (*Rhopalotria*), a supposed derivitive

TABLE 1. Estimated age of the tribes of Scolytidae, based on genera known to be restricted to tropical areas. Tribes are considered pre-Tertiary if a tropical genus or a close geographical replacement genus occurs in Africa and also in South America (Column 3). More recent postseparation (of Africa and South America) distribution is added as indicated (Column 4).

Tribe	Pre-Tertiary[1]	Ancient origin	Distribution added after early Tertiary
Hylastini	0	Holarctic	No change
Hylesinini	+	Old World	South America (from Africa), North America (from Asia)
Tomicini			
a. *Xylechinus* allies	+	South America	Worldwide
b. *Dendroctonus* allies	+	Worldwide in *Araucaria*	Worldwide
Prixosomini	+	Africa–South America	No change
Hyorrhynchini	0	Oriental	No change
Diamerini	0	Africa	Southern Asia to Australia
Bothrostornini	0	South America	North America
Phloeotribini	0	South America	Australia (from South America); North America to Eurasia, from South America.
Phloeosinini	+	Africa–South America	Ancient to Eurasia; modern to North America
Hypoborini	+	Worldwide (or Africa–South America)	Relicts
Polygraphini	0	Africa	Europe and Asia, then to North America
Scolytini	0	South America	North America then to Eurasia
Ctenophorini	+	South America	North America
Scolytoplatypodini	0	Africa	Southern Asia
Micracini	+	South America–Africa	North America to Asia
Cactopinini	0	North America	No change
Carphodicticini	+	?	South America–Southern Asia
Ipini	+	South America–Africa	Worldwide
Dryocoetini	+	Africa	Worldwide
Crypturgini	0	Africa	North America, Eurasia
Xyloterini	0	Asia	North America
Xyleborini	+	Africa–South America	Worldwide
Xyloctonini	0	Africa	Asia
Cryphalini	+	Africa–South America	Worldwide
Corthylini	0	South America (African segment)	Worldwide

[1]Marked (+) if present in recognizable form prior to the beginning of the Tertiary on more than one land mass. Marked (0) if represented at the beginning of the Tertiary by a local representative or a precursor that was present on only one land mass.

of Belidae, have only one gular suture, not two as in other members of the Belidae-Oxycorynidae-Aglycyderidae (Proterhinidae) group. Because such a placement would be a radical departure from the traditional position of Platypodidae-Scolytidae within the Curculionoidea (which has been next to the Curculionidae), additional supporting evidence was sought. The following summary of information presented in the above sections was found. A functional, but degenerate, adult labrum occurs in Curculionoidea only in Anthribidae and Nemonychidae. Rudiments of a labrum are well marked in many Platypodidae and obscurely indicated in some primitive Scolytidae, but they are not indicated in other curculionoids known to me. Anthribidae and Nemonychidae have a maxillary lacinia separate from the galea; this character is shared by Platypodidae (Tesserocerini), Attelabidae, and Rhynchitidae; the lacinia and galea are fused in all other curculionoids. Most of those curculionoids having two gular sutures have a 4-segmented maxillary palpus; Attelabidae, some Rhynchitidae, and one Platypodidae share that character. In Anthribidae, Nemonychidae, Eobelidae (fossil), Scolytidae, and Platypodidae the mandible is apically pointed, the cutting edge mesal, the condyles are closer together and differently positioned, and the apical part of the hypostoma is of minimal size. In all other cur-

culionoids, the basal half of the mandible forms a cylinder that rotates on a horizontal axis between the condyles, the dentate cutting edge is distal and moves through a different arc, and the hypostoma is enlarged to give greater strength to the posterior condyle. Whereas the preponderance of adult characters support the suggested relationship, larval characters have not been found that separate some Curculionidae from some Scolytidae. The larvae of Platypodidae and Scolytidae are easily separated; however, it is by the same primary character that Anthribidae and Nemonychidae larvae are separated (see key to families below). Obviously the Platypodidae-Scolytidae are not part of the Curculionidae and occupy a more primitive position in phylogeny. Exactly where they branch from the main curculionoid stem is not yet clear, but it could be from an Eobelidae-like ancestor.

Within the Platypodidae-Scolytidae, three major phyletic units are evident. The smallest and most distinctive paraphyletic line is the Platypodidae (about 1,000 species). They lack socketed tibial denticles, have the terminal, protibial mucro formed from the middle one of three apical spines (as compared to *Protohylastes*), always have the posterior half of elytral interstriae 10 present, always have a primitive mechanism for locking the elytra in closed position, lack a spiculum gastrale, and contain members having the primitive characters cited in the above paragraph. The Scolytidae contain partial or complete departures from these characters. As indicated above, six rare tropical genera (containing a total of seven species) are intermediate between these families.

The other two major phyletic lines include the Hylesininae (about 2,000 species) and the Scolytinae (about 4,000 species). Although the most primitive members of the family undoubtedly are members of the Scolytinae, that subfamily also contains far more and greater specializations than do the Hylesininae. Because the Hylesininae are less diverse and depart less drastically from the primitive form, they are considered more primitive and paraphyletic; the Scolytinae are more specialized and contain the major evolutionary thrust of the family. Hylesinine evolution appears to have been oriented toward a bodytype that is subspherical to take advantage of the row of crenulations on the bases of the elytra; scolytine evolved toward cylindrical compaction that is more effective in deeper host tissues where the ambrosial habit was exploited.

Progess toward a more nearly spherical body form in Hylesininae was accompanied by straightening out (somewhat) the scutoscutellar and pleural sutures on the metathorax. This apparently modified the mechanism of flight such that flection between the metathorax and its postnotum was no longer necessary and that the intersegmental line (membrane) was lost, at least in the median area. Accompanying that change were: a reduction in the number of segments of the antennal funicle from seven to as few as three and changes in the antennal club from cone-shaped, with simple, transverse sutures, to flattened and with or without sutures in numerous combinations. The primitive mating system was monogamy, with the female initiating the new parental gallery. Limited departures from that system include male initiated monogamy and heterosanguineous polygyny (many Polygraphini) and consanguineous polygyny (*Sueus* in Hyorrhynchini). A recognizable phyletic sequence appears to progress from the primitive Hylastini through Hylesinini to Tomicini. Hyorrhynchini and Phrixosomini appear to have been derived independently on separate lines from the same basic stock as that group of tribes. Among those tribes with a fused postnotum, Bothrosternini and Diamerini appear to be geographical replacements of one another that arose from a common ancestor that was much more closely allied to the Ctenophorini-like ancestor of Scolytinae than to the immediate ancestral stock of the Hylastini-Hylesinini-Tomicini. Although the Phloeotribini and Phloeosinini are closely related to one another, they (as one unit) were probably derived from the Bothrosternini-Diamerini ancestral stock independently from the unrelated Polygraphini and Hypoborini. Differentiation of phyletic lines in the Hylesininae has progressed slowly; consequently, they are difficult to detect. In general body habitus, *Protohylastes* (Platypodidae) resembles primitive hylesininae very closely, but the legs and antennae do not. *Pycnarthrum* (Ctenophorini)

would be placed in Hylesininae except for its legs. A primitive relationship of Hylesininae to primitive Scolytinae and Platypodidae is clearly indicated in these genera.

Among the Scolytinae, the Ctenophorini, Scolytini, and Scolytoplatypodini are closely related to one another and were almost certainly derived from a common Ctenophorini-like ancestral stock. The Ctenophorini more nearly resemble *Protoplatypus* (Platypodidae) than do other members of this subfamily. Some *Cnemonyx* (allies of *galeritus*, Ctenophorini) have crenulations on the basal margins of the elytra as in Hylesininae. The four remaining clusters of tribes were probably derived from a Ctenophorini-like ancestor in the following pattern. Although there is no clear primitive connection to an ancestral group, Micracini and Catopinini are anatomically and biologically allied to one another. An advanced member of Micracini probably gave rise to the Xyloctonini-Cryphalini group, then a Cryphalini-like member gave rise to the Corthylini. The remaining tribes, Carphodicticini, Ipini, Dryocoetini, Crypturgini, Xyloterini, and Xyleborini (listed in ascending order of anatomical and biological complexity) were probably derived from another Micracini-like ancestor along the same (one) phyletic line of descent. Active major evolutionary thrusts appear to be in progress within the Dryocoetini, Xyleborini, Cryphalini, and Corthylini, which combined contain more than half the living species of Scolytidae.

METHODS

Although this project was conceived in 1949, serious work on it was not started until 1955. From 1955 to 1965, comparative anatomical studies were made of representatives of more than 100 selected genera of Curculionoidea, in addition to more than 60 genera of Scolytidae and Platypodidae. As the patterns of evolution began to emerge from those studies, a major effort was made to collect specimens and to gather behavioral and ecological data on species not previously known to me. More than 2,000 species of Scolytidae and 300 species of Platypodidae were collected from North and South America, Europe, Asia, Australia, and New Guinea. In addition, visits were made for the purpose of studying types and comparing them and other specimens to my material at museums in the United States, Canada, Mexico, Venezuela, England, Austria, Finland, USSR, India, Japan, Australia, and Papua-New Guinea. There visits included stays of a month or more at the British Museum (Natural History), the Schedl Collection (both at Lienz with Schedl in 1965 and at Vienna in 1983), and the Forest Research Institute, Dehra Dun, India (where more than 40,000 Indian specimens were sorted to species in addition to studies of the types). It is estimated that well over 400,000 specimens of Scolytidae and Platypodidae were examined. From those museums not visited in person by me, types and other specimens were obtained for study through loan. Except as noted below under Incertae Sedis, all existing type-species for all named genera and subgenera were examined and, where type-specimens have been designated, the type-specimen of those species were also studied. The basis for recognition is given under each species and synonym below.

Except at Helsinki (Finland), Leningrad and Moscow (USSR), Bulolo (Papua-New Guinea), and Sydney (Australia), where local museum equipment was used, the studies were made using an American Optical Company stereoscopic microscope, model 25, equipped with an occular grid, at magnifications of 10, 40, 80, and 160X. All measurements were made at 10X and excluded the head (in measurements of body length).

Authentic specimens of the type-species of several genus-group names assigned to the Scolytidae were not examined during the course of this study. These species fall into two categories: (1) those for which the types or other authentic specimens could not be found and are presumed lost, and (2) fossil species.

The types of four genera could not be found. These included:

1. *Allarthrum* Hagedorn (1912:355), based on *A. kolbei* Hagedorn (1912:355), from Peterhafen, Deutsch New Guinea. The type(s), 1.5 mm in length, was deposited in the Kgl. Zoolog. Museum Berlin but cannot now be found. The illustration of the antenna (Hagedorn 1912:Fig. 5) is of a *Cryphalus* species. It is provisionally listed as a synonym of *Cryphalus*.

2. *Bufonus* Eggers (1919:231), based on *B. obscurus* Eggers (1919:231) from Amani, Ost-Afrika. The unique holotype, 1.5 mm, was lost with the Hamburg Museum in 1944. The antennal funicle was described as 2-segmented, the club elongate, with three transverse sutures; the scutellum was not visible, the basal margins of the elytra were sharply rounded, and the elytral sculpture was pronounced and unique. Except for the absence of crenulations on the basal margins of the elytra, this genus would be placed in Hypoborini. A more detailed knowledge of the fauna of East Africa is needed before it can be correctly placed in classification.

3. *Toxophorus* Eggers (1920b:119; preoccupied, renamed *Toxophthorus* Wood), based on *T. africanus* Eggers (1920b:119) from Deutsche-Ostafrika. The unique holotype, 3.0 mm, was lost with the Hamburg Museum in 1944. The antennal scape was elongate, the funicle was 5-segmented, the club was flattened, with a suture near the apex, and the frons was impressed above the eyes. This genus almost certainly is in the Dryocoetini, possibly near *Tiarophorus* or *Xylocleptes*.

4. *Pseudomicracis* Eggers (1920a:36), based on *P. elsae* Eggers (1920a:36) from Dares-Salaam, Ostafrika. The unique female holotype, 1.5 mm, was lost with the Hamburg Museum. The frons was impressed, the antenna was similar to *Micracis*, the scape was triangular, with long hair on the outer angle, and the sutural apex of the elytra mucronate. Because only one known genus bears the combination of characters described by Eggers, his name is associated with those African species previously referred to the American genus *Micracis*. As such, this genus is recognizable and is treated below under the name *Pseudomicracis*.

Of the six fossil genera that have not been previously placed in synonymy under older names of modern genera, four are from Baltic amber, one is from Burmese amber, and one is from sedimentary deposits. These include:

1. *Carphoborites* Schedl (1947:32) was based on *C. keilbacki* Schedl (1947:32) and *C. posticus* Schedl (1947:33), both from Baltic amber (*Charphoborites* was a lapsus calami). From the descriptions, I see no reason to separate these species from *Carphoborus*; however, I have not examined the specimens.

2. *Hylescierites* Schedl (1947:29) was based on *H. granulatus* Schedl (1947:30) from Baltic amber. From the photograph of the holotype and the original description, I see no reason for separating this species from *Hylurgops*.

3. *Taphramites* Schedl (1947:41) was based on *T. gnathotrichus* Schedl (1947:42) from Baltic amber. From the description, it appears that this species should be placed in Dryocoetini, probably in or near *Dryocoetes*. I have not examined the specimen.

4. *Xylechinites* Hagedorn (1907:120) was based on *X. anceps* Hagedorn (1907:120) from Baltic amber and was redescribed and illustrated by Schedl (1947:30–32). The descriptions and photograph of the holotype indicate that this species is a Tomicini near or in *Xylechinus*. I have not examined the specimen.

5. *Cryphalities* Cockerell (1917:368) was based on *C. rugosissimus* Cockerell (1917:368) from Burmese amber. Because no usable characters were included, the original description gives no clue as to where this species should be placed. It is assumed that Cockerell was correct in assigning it to Cryphalini. I have not examined the specimen.

6. *Xyleborites* Wickham (1913:26) was based on *X. longipennis* Wickham (1913:26) from the Wilson Ranch near Florissant, Colorado. The author indicated that this species, 2.2 mm in length, resembled *Xyleborus pubescens*. Essential characters were not described. The specimen was not examined by me.

Pityophthoridea Wickham (1916:18) and *Adipocephalus* Wickham (1916:16) are not considered to be members of the Scolytidae.

SYSTEMATIC SECTION

Although some obvious unanswered questions remain as to the exact position of Platypodidae and Scolytidae within the Curculionoidea, the following key is presented for the identification of families. The presence of complete pregular sutures and the mandible structure of Platypodidae and Scolytidae are obviously more primitive than the absence of these sutures and the specialized mandibular structure of Belidae and Oxycorynidae, but the single gular suture and presence of larval epipharyngial rods are more advanced than

the two gular sutures and absence of the rods in Belidae. The long subcortical history and very small body size of Platypodidae and Scolytidae have had an obvious effect on their anatomy that complicates interpretation of their position in phylogeny.

This key to families of the Curculionoidea is tentative. A thorough reexamination of the Belidae-Aglycyderidae-Oxycorinidae groups is needed to determine the significance of single vs. double gular sutures, the precise position of character gaps that separate families, etc. Another area of concern is the section of the key in couplets 11 and 12. Characters to separate these three taxa are weak, but, in view of the large number of species to be classified herein, perhaps the recognition of these three families is justified. Among more than 150 genera of Curculionidae (in the sense used here) dissected by me, I saw three possible divisions of this family. These included (1) the Cossoninae-Rhynchophorinae, (2) the broadnose weevils, and (3) all others. It is recognized that some equally distinct groups may exist that were not seen by me, but a thorough comparative anatomical study should precede their recognition. Following my study, I seriously doubt that even one-third of the 75 or more subfamilies that have been recognized within Curculionidae deserve this rank; most are worthy of no more than tribal status.

Key to the families of Curculionoidea

1. Adult: two gular sutures present or rudiments of them evident (only one gular suture and a postgula present in several Belidae and *Rhopalotria* of Oxycorynidae); maxillary palpi 4-segmented; abdominal segments free (except 3–6 connate in Anthribidae); antennae usually orthocerous, scape little longer than succeeding segments, club loosely 3-segmented. Larva: epipharyngeal rods absent; maxillary palpi 3-segmented, rarely 2-segmented; thoracic legs present; frontal sutures reaching articulating membrane of mandible; two folds in each abdominal tergum 2

— Adult: one gular suture extending from minute postgula at margin of foramen magnum to posterior tentorial pits (usually where base of rostrum meets head); maxillary palpi 1- to 3-segmented (4-segmented in one Platypodidae, some Rhynchitidae, and all Attelabidae); abdominal segments free or partly connate in some groups; antennae frequently geniculate, a definite club usually present (orthocerous in Brenthidae; intermediate in Ithyceridae, Apionidae, some Platypodidae, and a few Sc. 'ytidae). Larva: epipharyngeal rods present; maxillary palpi 1- or 2-segmented (3-segmented in Brenthidae and Rhynchitidae); thoracic legs absent (present in Brenthidae and Ithyceridae); frontal sutures not reaching articulating membrane of mandible (except Brenthidae, Apionidae, Ithyceridae, some Platypodidae); two to four folds in each abdominal tergum 6

2(1). Adult: labrum distinct and separate (except absent in *Bruchela* of Anthribidae); maxillary palpi flexible, lacinia forming a distinct element (see also Rhynchitidae and Tesserocerini in Platypodidae). Larva: mandibles with a distinct mola 3

— Adult: labrum fused or lost; maxillary palpi rigid; maxilla without a separate lacinia. Larva: mandibles without a distinct mola 4

3(2). Adult: gular sutures rudimentary, represented only at margin of foramen magnum or totally lost; tentorium largely or entirely obsolete; proventriculus developed; lateral margins of pronotum acute (rounded in *Bruchela*); inner margin of elytra with a flange near costal margin; cavities of mesocoxae broadly closed outwardly by sternum, visible abdominal sterna 1–4 connate. Larva: clypeus distinct from frons, or head deeply retracted; mandibles without ventral process in addition to mola (includes the distinct subfamily Bruchelinae) .... **Anthribidae**

— Adult: gular sutures extending from margin of foramen magnum to posterior tentorial pits; tentorium present; proventriculus indistinct; inner margin of elytra without a flange near costal margin; mesocoxae not or imperfectly closed outwardly by sternum; abdominal sterna free. Larva: clypeus usually fused to frons; head not deeply retracted into prothorax; mandibles with a ventral process in addition to mola .... **Nemonychidae**

4(2). Adult: gular sutures longer, extending to posterior tentorial pits; partial pregular sutures occasionally present in female near apex of rostrum; at least three genera with large postgula and short median gular suture; antennae filiform or nearly so, inserted laterally remote from base of rostrum; inner margin of elytra with a flange near costal margin; wing with five anal veins in main group complete to base; tarsi normal, pseudotetramerous; lateral margins of pronotum transversely rounded. Larva: maxillary palpiger well developed; thoracic spiracle intersegmental ... . **Belidae**

— Adult: gular sutures usually short (a large postgula and one median gular suture in some Oxycorynidae), externally visible near foramen magnum or else lateral margins of pronotum acute; antennae inserted at or near base of rostrum; either antennae clubbed or tarsi pseudotrimerous; inner margin of elytra with-

out a flange near costal margin; wings with fewer than five anal veins or else bases of elytral veins incomplete. Larva: maxillary palpiger usually not evident; thoracic spiracle in mesothorax 5

5(4). Adult: tarsi pseudotrimerous, segment 2 bilobed; antennal insertion at base of rather short rostrum; antenna filiform, not clubbed; proventriculus well developed. Larva: maxillary palpiger not distinct . . . . **Aglycyderidae** (= Proterhinidae)

— Adult: tarsi pseudotetramerous, segments 2 and 3 bilobed; antennal club 2- or 3-segmented; (a large postgula and at least a partial median gular suture present in at least *Rhopalotria*); lateral margins of pronotum acute; antennal insertion at base of long rostrum, on ventral face; proventriculus poorly developed. Larva: palpiger distinct . . **Oxycorynidae**

6(1). Adult: pregular sutures present and reinforced internally by massive apodemal ridges; rostrum short to nonexistent; tibiae armed on apical or lateral margins by a series of spines and/or socketed teeth of setal origin, corbels never present; hypostomal area small, never armed by a large spine, posterior mandibular condyle more anterior in position; axis of mandibular hinge oblique to transverse, cutting edge on mesal margin (Fig. 8); some members (Tesserocerini) with a separate lacinia 7

— Adult: pregular sutures absent, with no indication of supporting internal apodemal structure (longitudinal ridges giving rigidity to rostrum are not reinforced internally and should not be confused with true pregular sutures); rostrum variable, long to very short; lateral margins of tibiae unarmed (except for simple spines in some Cossoninae), corbels commonly present; hypostomal area larger, commonly armed by a large spine, posterior mandibular condyle more posterior in position (Fig. 8); axis of mandibular hinge parallel to body axis, cutting edge on apical margin; separate lacinia never present (except some Rhynchitidae and all Attelabidae) 8

7(6). Adult: tarsal segment 1 elongate, usually longer than 2–5 combined (except shorter in *Protoplatypus*, *Protohylastes*, *Coptonotus*, *Scolytotarsus*); tibiae armed on apical and/or lateral margins by one or more spines, never by socketed denticles, apical mucro formed by middle apical spine (as compared to *Protohylastes*); male spiculum gastrale absent; antennal club solid, unmarked by sutures (feebly indicated in *Coptonotus*); head about as wide as pronotum; pronotum with distinct lateral constriction near middle; when visible, scutellum often reduced, declivous, usually with not more than apex attaining (flush with) elytral surface; metepisternum very elongate, its anterior margin straight, its anteroventral angle neither displaced caudad nor extended ventrad; mesepimeron flat, vertical; mesepisternum moderately to greatly enlarged, varying from flat to inflated; eyes convex, never truly emarginate; pronotum never armed by asperities. Larva: clypeus fused to frons in all except primitive genera; frontal sutures reaching articulating membrane of mandible or not . . . . **Platypodidae**

— Adult: tarsal segment 1 about equal in length to 2 or 3; tibiae armed on apical and/or lateral margins either by spines or socketed denticles, apical mucro formed by mesal element (compared to *Protohylastes* structure); male spiculum gastrale present; antennal club variable, with or without sutures; head narrower than pronotum; pronotum almost never with constriction near middle; when visible, scutellum usually flush with elytral surface, often flattened; metepisternum stout to elongate, its anterior margin usually procurved, its anteroventral angle displaced slightly caudad and distinctly extended ventrad; mesepimeron flat, oblique; mesepisternum smaller, declivous cephalad; eyes more nearly flat against head, often emarginate to divided; pronotum often asperate. Larva: clypeus distinct, separate from frons; frontal sutures never reaching articulating membrane of mandibles . . . . **Scolytidae**

8(6). Adult: labial palpi inserted ventrally on mentum; head frequently constricted behind eyes; antennae never geniculate, inserted dorsally or laterally at base or middle of rostrum, club absent to moderately distinct; proventriculus without sclerotized plates. Larva: frontal sutures reaching articulating membrane of mandibles 9

— Adult: labial palpi inserted apically; antenna straight or geniculate, inserted laterally at middle or near apex of rostrum, club 1- to 3-segmented, loose to compact, small to large. Larva: frontal sutures either reaching or not reaching articulating membrane of mandibles 10

9(8). Adult: maxillary palpi 4-segmented, galea and lacinia distinct; mandibles often dentate on outer margin; labial palpi 1- or 3-segmented (rarely absent); elytra with a scutellary striole; notosternal suture short, laterally reflexed; hind wing usually with four anal veins, radial cell well developed; sterna 3–6 rarely free, 3–4 connate in some, 3–6 connate in most; cap piece of male tegmen simple, setose; malpighian tubules grouped three on each side of alimentary canal; more than two ovarioles in each ovary. Larva: legs absent, two or more stemmata present on each side of head; antenna usually 2-segmented; maxillary palpi 2- or 3-segmented; abdominal terga with two folds . . . . **Attelabidae**

— Adult: maxillary palpi 3-segmented, galea and lacinia fused; mandibles never dentate on outer margins; elytra never with scutellary

striole; notosternal suture well developed and usually extending almost to anterior margin; hind wing with three or fewer anal veins, radial cell not evident; sterna 3–4 connate and much longer than 5–6; cap piece of tegmen bilobed. Larva: rudimentary, segmented legs present; stemmata absent; antenna 1-segmented; maxillary palpi 3-segmented; abdominal terga with three to four folds .... **Brenthidae**

10(8). Adult: maxillary galea and lacinia distinct, palpi 3- or 4-segmented; metepimeron subtransversely carinate and interacting with humeral angles of elytra to aid in locking elytra in position, metepisternal locking element not developed and its interlocking flange at this point on inner costal margin of elytra absent; antenna straight, club loosely 3-segmented; abdominal sterna 3 and 4 connate, suture distinct. Larva: median area on posterior part of head overlapped by prothorax; maxillary palpi 2- or 3-segmented; two basal sensillae on labrum; frontal sutures complete but indistinct; abdominal terga with two folds .... **Rhynchitidae**

— Adult: maxillary lacinia usually fused to galea, palpi 2- or 3-segmented; metepisternum carinate, fitting flange on inner margin of elytra near humeral angle, metepimeron not carinate; antenna straight or geniculate, clubbed or not. Larva: posterior part of head free in median area; maxillary palpi 1- to 3-segmented; no basal sensillae on labrum 11

11(10). Adult: abdominal tergum 8 longitudinally grooved for reception of inwardly raised elevation at suture near apex of elytra; tergum 8 bearing a pair of spiracles; maxillary palpi 3-segmented, but largely retracted into palpifer; antenna not geniculate. Larva: rudimentary, segmented legs present; maxillary palpi 2-segmented; 3 stemmata present .... **Ithyceridae**

— Adult: abdominal tergum 8 not grooved, spiracle absent; maxillary palpi 2- or 3-segmented, usually not retracted into palpifer . 12

12(11). Adult: either antenna not geniculate, or if geniculate then trochanters long, cylindrical, femur remote from coxa, attached to apex of trochanter; ventral surface of mentum usually with projecting setae; proventriculus poorly developed. Larva: frontal sutures extending to articulating membrane of mandibles; abdominal terga with two folds .... **Apionidae**

— Adult: antenna usually geniculate; trochanters triangular, femur attached to side of trochanter, sometimes almost touching coxa; ventral surface of mentum without projecting setae; proventriculus usually well developed. Larva: frontal sutures not reaching articulating membranes; abdominal terga with two to four folds .... **Curculionidae**

Family Scolytidae Latreille

Scolytarii Latreille [1807:273, Type-genus: *Scolytus* Geoffroy 1762, see also China 1962]

The family Scolytidae is compromed of a group of more than 6,000 small to minute species. Whereas the preponderance of species are tropical, a few of them reach the northern and southern limits of tree distribution near the polar regions. They are unique in that loosely pair-bonded adult parents bore into subcortical tissues of their host (usually) before mating or oviposition occur. Eggs are variously placed in the galleries, and the larvae either expand the parental mines or form individual galleries while the parents defend the outer entrance to the tunnel. Thus, the beetles are essentially internal plant parasites that spend virtually their entire lives secreted within the tissues of the host. The ephemeral habitat they occupy is the unthrifty, weakened, or dying tissue of woody plants; only one generation is completed in each host unless a large tree that is succumbing progressively is involved. Because of the very brief period this habitat is open to them, efficient means of locating a host, recruiting a population to subdue it, and overcoming host resistance are mandatory. This is accomplished through sensitivity to odors emitted by trees under stress, by a complex system of pheromones, and by mutualistic relationships with fungi. Several of the most efficient species, with respect to meeting these challenges, compete with man for timber and horticultural resources and present a very real threat to human economy. Most woody plants, a few herbaceous plants, and many fruits and nuts are infested by these insects. The adjustments they have made in their mating systems, utilization of food resources, and adaptive radiation form a classic example of biological diversity.

Key to the Subfamilies and Tribes of Scolytidae (Modified from Wood 1978)

1. Each basal margin of elytra procurved and armed by a series of marginal crenulations (Fig. 16) (or less commonly by a continuous elevated costa in some Bothrosternini, Diamerini, Polygraphini), usually with a scutellar emargination between them; scutellum usually small and rounded or depressed, absent in some groups; pronotum weakly if at all declivous on anterior half, usually unarmed

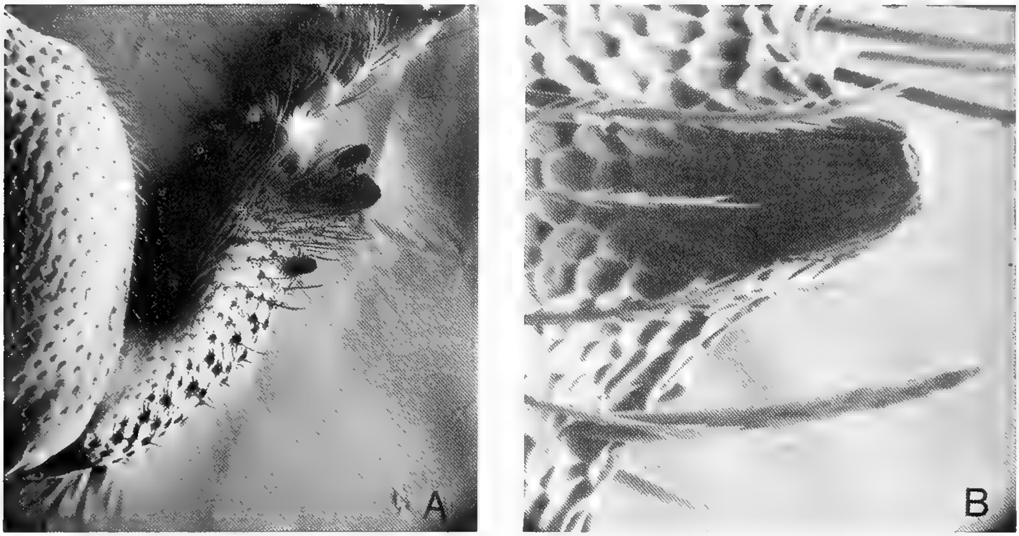


Fig. 24. *Eupagiocerus dentipes* Blandford, protibia: A, posterior face showing the bifid spine on the lateral, apical angle and small socketed denticle; B, an enlargement of the socketed denticle.

but crenulations sometimes present on anterolateral areas; head usually visible from above, somewhat wider; protibia usually wider; scales or deeply divided setae a common feature (subfamily HYLESININAE) 2

— Basal margins of elytra forming a straight, transverse line across body (Fig. 17), unarmed, rarely (some Scolytini, Ctenophorini, Cryphalini) with a weakly elevated continuous line; scutellum usually large, flat (rarely absent or highly modified in some Xyleborini); pronotum weakly to strongly declivous on anterior half and usually armed by many asperate crenulations, particularly on median half (Figs. 31, 46, 52); head usually partly or entirely concealed from dorsal aspect, somewhat narrower; protibia usually narrower; scales or deeply divided setae an uncommon feature (subfamily SCOLYTINAE) 12

2(1). Scutellar area of metanotum and its postnotum separated by a suturelike intersegmental membrane (Fig. 23, pts. 43, 45); posterior part of scutoscutellar suture strongly curved mesad to a point near crest of scutellar groove then continuing cephalad parallel to this costa for about two-thirds of metanotum length (Fig. 23, pt. 43) (except much less in Phrixosomini and Hyorrhynchini); metapleural suture descending subvertically from pleural wing process to metepisternal groove formed to receive corresponding costal groove and flange of elytron then abruptly angled and continued caudad along this groove to a point near pleural coxal process (Figs. 18, 23 pt. 44); scutellum visible; funicle 6- or 7-segmented or if 5-segmented (*Sueus*) then eye divided, male frons not impressed, and antennal club symmetrical 3

— Scutellar area of metanotum and its postnotum completely fused on at least median third, intersegmental suture usually obsolete (Figs. 21, 23 pt. 41); scutoscutellar suture less strongly curved, approaching costa of scutellar groove more gradually and continuing cephalad parallel to it for less than half length of metanotum (Fig. 23, pt. 41) (it never reaches margin of this groove in some groups; metapleural suture sometimes as described above, but more commonly running a more direct route from pleural wing process to pleural costal process, often remote from locked position of costal margin of elytra for most or all of its course (Figs. 21, 23 pt. 41); scutellum either not visible or if visible then funicle 5-segmented and male frons impressed (Bothrosternini with 6-segmented funicle but with a distinctive protibia, Fig. 24) 7

3(2). Eye entire to feebly emarginate; scutoscutellar suture parallel to costa of scutellar groove for two-thirds length of notum; precoxal ridge on prothorax present (Fig. 20) or absent; antennal funicle 5- to 7-segmented 4

— Eye completely divided by an emargination, halves widely separated; scutoscutellar suture remote from costa of scutellar groove; crenulations on basal margins of elytra low, often poorly formed; precoxal ridge on prothorax never present; antennal funicle usually 6-segmented (5-segmented in *Sueus*) 6

4(3). Prothoracic precoxal area rather large, its lateral margins strongly, sharply elevated from anterior margin to coxae (Fig. 20); crenulations on elytral bases usually poorly developed; antennal funicle 7-segmented, club conical, segment 1 often as long as others combined; head somewhat prolonged, subrostrate, frons never sexually dimorphic; eyes

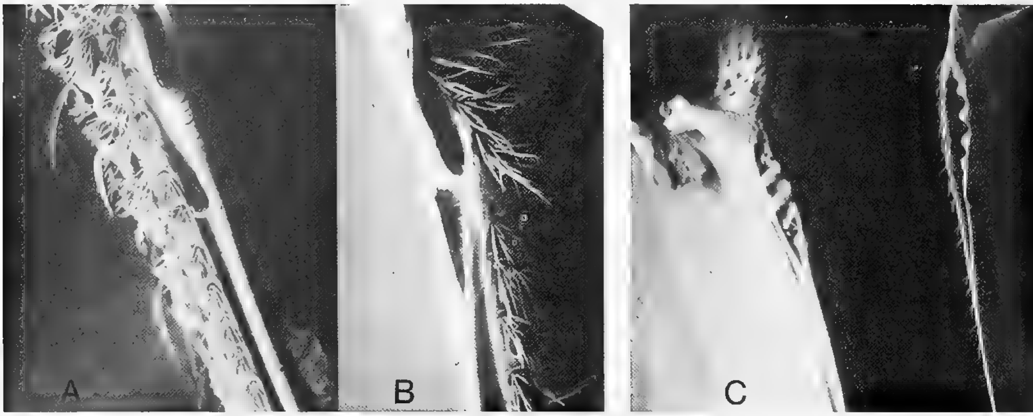


Fig. 25. Mesal aspect of elytral base: A-B, *Pseudohylesinus nebulosus* (LeConte), groove nearest pubecent surface continues to base without interruption (ignore the tiny grain of frass trapped in the groove in A); C, *Phloeosinus cristatus* (LeConte), groove near base interrupted by a series of interlocking nodules and cavities.

entire, rather short; Northern Hemisphere, except introduced elsewhere; in Pinaceae . . . . **Hylastini**

— Prothoracic precoxal piece small, short, its lateral areas elevated or not; crenulations on elytral bases more conspicuously elevated, forming a definite row (except confused in *Dactylipalpus*); antennal funicle variable, 5- to 7-segmented, club weakly to moderately flattened; head less distinctly rostrate, male frons usually impressed, eye oval to elongate, entire to feebly emarginate 5

5(4). Pronotum asperate on anterolateral areas (except *Hylastinus*); prothorax with elevated costate ridge from coxa to anterior margin (weaker than in Fig. 20); antennal funicle 6- or 7-segmented; mesal surface of elytra at base of suture immediately behind scutellum with an interlocking series of nodules and cavities (Fig. 25-C), this lock interrupts groove and flange of suture (not visible when elytra in locked position); worldwide . . . . **Hylesinini**

— Anterolateral areas of pronotum unarmed; precoxal costa on prothorax absent; funicle 5- to 7-segmented; mesal surface of elytra at suture with interlocking groove and flange continuted to base without a series of nodules or cavities immediately behind scutellum (Fig. 25-A-B); worldwide . . . . **Tomicini**

6(3). Protibia armed on outer apical margin by several socketed denticles of approximately equal size; procoxae contiguous; frons convex, not sexually dimorphic; antennal scape elongate, suture 1 of club partly septate; pronotum never armed by asperities; America, Africa . . . . **Phrixosomini**

— Protibia with outer apical angle produced into one conspicuous spine reaching level of tarsal insertion, outer margin without any socketed teeth; procoxae rather widely separated; male frons broadly impressed (except in dwarfed *Sueus*), female frons convex; antennal scape either long or short, club aseptate; pronotum either with or without asperities in anterolateral areas; southeast Asia . . . . . . **Hyorrhynchini**

7(2). Lateral margins of pronotum usually subacutely elevated, costate (as in Fig. 12); mesepimeron moderately to very large, its dorsal portion usually grooved for reception of elytral base; scutellar shield under base of elytra large, extending posteriorly beyond visible scutellum (Fig. 26); scutoscutellar suture remote from costa of scutellar groove to its base; outer apical angle of protibia often with only one major recurved spine (Fig. 7); Africa, southeast Asia to Australia . . **Diamerini**

— Lateral margins of pronotum rounded (Fig. 16) (subcostate in a few neotropical Bothrosternini, Fig. 11); mesepimeron not enlarged or grooved (feebly grooved in *Aricerus*); scutellar shield beneath elytra small if present, not extended caudad beyond visible scutellum (Figs. 18, 21); scutoscutellar suture near and parallel to costa of scutellar groove on at least anterior fourth of metanotum 8

8(7). Outer apical angle of protibia with a curved bifid process, meso- and metatibiae with one or two (usually smaller) curved spines on outer apical angle extending beyond level of spine on inner apical angle (Fig. 24); pronotum smooth or longitudinally strigose; funicle 6-segmented; lateral prosternal area usually subacutely elevated from coxa to anterior margin; anterior coxae rather widely separated; crenulations on elytral bases rather small or (rarely) replaced by a continuously elevated costa; eye entire; America . . . . **Bothrosternini**

— Outer apical margin of protibia armed by several teeth of about equal size (except *Aricerus* in Phloeotribini), none of them extending be-

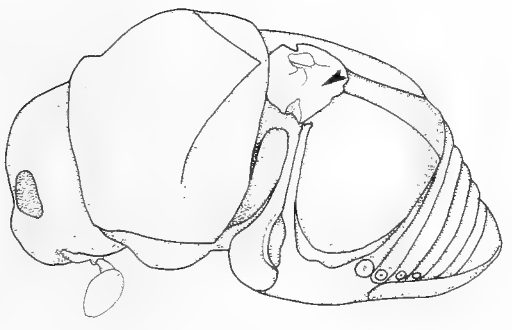


Fig. 26. Diagram of *Sphaerotrypes globosus* Blandford, with elytra removed, showing enlarged scutellar plate that lies below the base of the elytra.

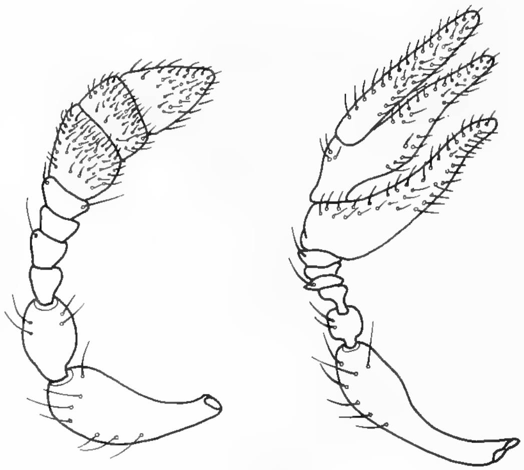


Fig. 27. Antenna of *Phloeotribus*: A, *rhododactylus* (Marsham); B, *caucasicus* Reitter.

yond tarsal insertion; funicle 4- to 7-segmented; prosternal area with margins rounded, costa obsolete; eye varying from entire to emarginate to divided 9

9(8). Scutellum visible, elytral bases notched for its reception; tarsal segment 3 stout, usually somewhat bilobed (except slender in *Chramesus*); mesal surface of elytra at suture immediately behind scutellum with a series of interlocking nodules and cavities (Fig. 25-C) 10

— Scutellum obsolete, elytral bases only slightly if at all emarginate at suture (Fig. 17); tarsal segment 3 slender; mesal surface of elytra at suture usually without a special lock, groove and flange extend to base at position of scutellum (degenerate in Fig. 25-A-B) 11

10(9). Antennal club constricted at sutures and movable at intersegmental lines (Figs. 16, 27); Holarctic, Neotropical, and Australian .... **Phloeotribini**

— Antennal club immovably, broadly fused at sutures, sutures often partly or entirely obsolete; worldwide .... **Phloeosinini**

11(9). Eye emarginate or entirely divided; pronotum never armed by asperities; crenulations at bases of elytra more widely distributed, extending laterad beyond interstriae 5 (Fig. 16); funicle 5- or 6-segmented; scutoscutellar suture passing near and parallel to costa of scutellar groove on anterior fourth of metanotum; Northern Hemisphere and Africa ... . **Polygraphini**

— Eye sinuate or entire; pronotum armed by a few scattered or clustered asperities; crenulations at bases of elytra restricted to area between suture and interstriae 5; funicle 3- to 6-segmented; scutoscutellar suture remote from costa of scutellar groove on anterior fourth of metanotum; almost worldwide .... **Hypoborini**

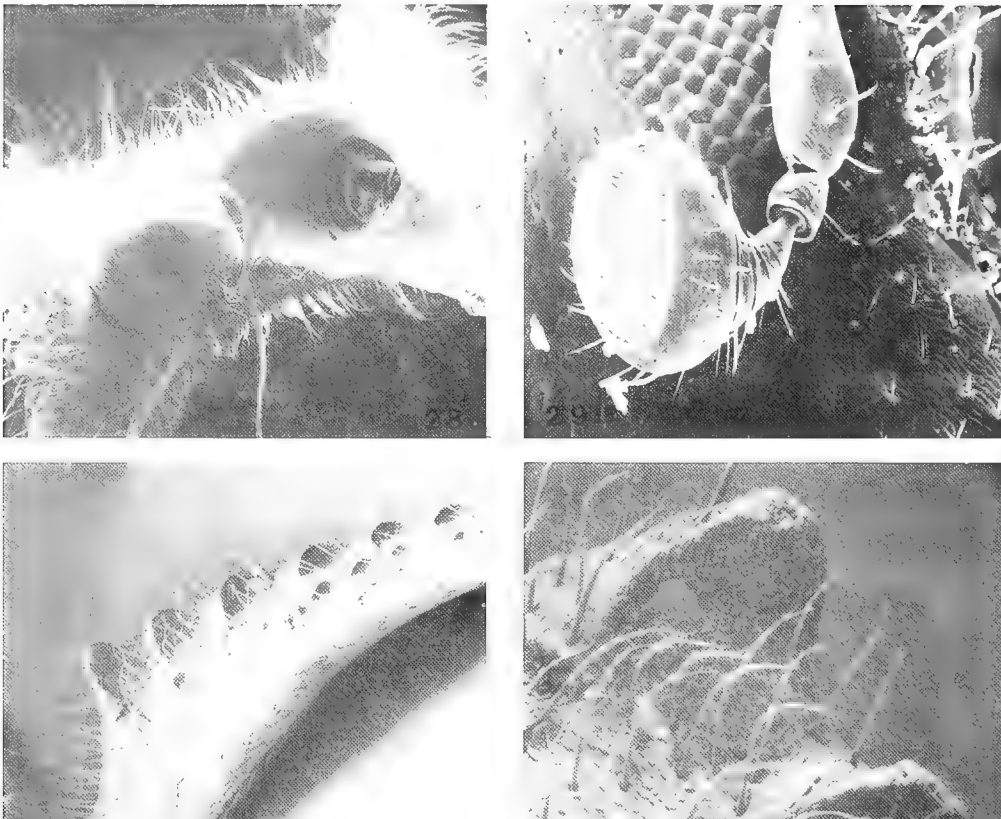
12(1). Lateral margins of pro- and metatibiae unarmed except for a single, apical, spinelike process that curves toward and extends beyond process of inner apical angle (Fig. 7, *Camptocerus*); lateral margins of pronotum subacutely elevated, costate; pleural suture descending subvertically from pleural wing process to groove receiving groove and flange on costal margin of elytra, at this point suture turns abruptly and follows groove caudad to metapleural coxal process (Fig. 23, part 46); funicle 7-segmented, sutures of antennal club strongly procurved or obsolete; Holarctic and Neotropical .... **Scolytini**

— Lateral margin of protibia armed by more than one denticle, none of which exceed or curve toward inner apical process; pleural suture less strongly angulate, groove receiving flange of costal margin of elytra displaced ventrad from course followed by pleural suture (Fig. 23, part 42); lateral margins of pronotum subacutely raised or not, antenna variable .. 13

13(12). Metepisternum visible throughout its length, slightly more than its dorsal half covered by elytra when in locked position, either with a conspicuous groove for reception of costal flange throughout its length or else groove represented at its anterior end by a denticulation or costate remnant near anterior end of metepisternum (Fig. 23, parts 42, 44, 46); antennal club varying from flat to obliquely truncate (Fig. 29) 14

— Metepisternum largely covered by elytra, its groove for reception of costal flange obsolete, a small, transverse callus (Cryphalini, Fig. 31) or a small transverse groove (Corthylini, Figs. 23, part 47, and 32) at anterior end of metepisternum; antennal club strongly flattened; antennal club never obliquely truncate 24

14(13). Lateral margins of pronotum subacutely elevated, basal margins of elytra usually finely elevated; procoxae rather widely separated except contiguous in Xyloctonini; protibia



Figs. 28-32. Scolytidae parts: 28, *Ips woodi* Thatcher, ventral aspect of prothorax showing contiguous coxae, left coxa removed (ignore the plant fiber between the coxae); 29, obliquely truncate antennal club of *Dryocoetes confusus* Swaine; 30A, posterior face of protibia of *Scolytoplatypus papuanus* Eggers showing unsocketed spines on lateral margin, B, enlargement of spines 1 and 2; 31, dorsal aspect of posterolateral area of prothorax of *Cryphalus ruficollis* Hopkins, with left elytron removed to expose anterolateral area of metathorax (arrow points to the groove that is partially replacing the metepisternal spine; 32, left pleuron of *Corthylus panamensis* Blandford, with elytron removed; upper arrow points to pleural suture, lower one to the groove that has entirely replaced the metepisternal spine.

with prominent outer apical process recurved (Fig. 7, *Scolytodes*), usually extending beyond tarsal insertion, posterior tibia tapered on apical third and armed by several small socketed denticles; funicle 6- or 7-segmented; tarsi often retractible into tibial grooves 15

— Lateral and basal margins of pronotum rounded (except *Cnestus*); procoxae subcontiguous (except most Micracini and a few Xyleborini); protibia with outer apical angle inconspicuous, armed by several small socketed denticles; funicle 2- to 6-segmented; tarsi not retractible (except in *Eccoptopterus*) 17

15(14). Eye divided or nearly so by a very deep emargination; antennal club flat, usually enlarged, with sutures strongly procurved; abdomen conspicuously ascending toward apex (not always clear in *Ctonoxylon*); tarsi always retractible into tibial grooves; Africa and southern Asia .... **Xyloctonini**

— Eyes entire to shallowly sinuate on anterior margin; antennal club flat, usually smaller, more slender, sutures variable, if present; abdomen horizontal; tarsi retractible or not ... 16

16(15). Antennal club with one or more sutures indicated by grooves, setae, or septae; scutellum large, flat; America; mostly phloeophagous, never mycetophagous .... **Ctenophorini**

— Antennal club unmarked by sutures; pronotum with sides strongly constricted on posterior half; scutellum absent (a small scutellum present in *Scolytoplatypus congonus*); Africa to Asia and New Guinea; mycetophagous ... . **Scolytoplatypodini**

17(14). Procoxae moderately separated; protibia with sides parallel, armed by denticles only on apical margin or posterior face; funicle 6-segmented (5-segmented in one African genus); female frons often concave, male frons rarely concave (except two *Pseudothysanoes*); Africa and America, one species in Asia .... **Micracini**

— Procoxae contiguous (except Carphodicticini, some Xyleborini); protibia much wider apically, armed on lateral margin by several denticles; female frons rarely concave (a few Dryocoetini), male frons often concave; funicle 2- to 5-segmented, 6-segmented in *Tiarophorus* 18

18(17). Male frons strongly excavated, epistoma armed by a pair of (usually) fused horns of enormous size (Fig. 47); funicle 5-segmented, club often small and feebly flattened; eye small, entire; pronotum with summit near basal margin, projecting back over scutellum in some species; western United States and Mexico .... **Cactopinini**

— Not fitting above combination of characters . 19

19(18). Meso- and metathoracic tibiae more slender, more abruptly narrowed on apical fourth, lateral and apical margins armed by fewer, coarser teeth; eye sinuate to shallowly emarginate (divided in *Tiarophorus*, Dryocoetini, Africa); pronotum sometimes with a raised line on basal or lateral margin; pregular area not depressed; sexes of similar size and body form (except male dwarfed and deformed in *Coccotrypes* and *Ozopemon*); habits varied but never woodboring or mycetophagous ... 20

— If eye completely divided into two parts and antennal funicle 4-segmented then male frons deeply excavated and male equal in size to female; if eye emarginate (or if divided and funicle 5-segmented) then male dwarfed, deformed, and flightless and female meso- and metathoracic tibiae expanded to just beyond middle then arcuately tapered to apex, its apical two-thirds on outer margin armed by a row of numerous small, closely set teeth of equal size, these usually supplemented in same row by submarginal hair on posterior face; male pronotum highly modified; pregular area depressed (except *Premnobius*); woodboring, mycetophagous 23

20(19). Pronotum rather strongly, laterally constricted on posterior half, anterior half not declivous and never armed by asperities; anterior coxae moderately separated; antennal club strongly flattened, marked by two sutures, sutures on posterior face almost equal to those on anterior face; South America and India to Ceylon (Sri Lanka) .... **Carphodicticini**

— Pronotum not constricted, sides straight to arcuate, anterior half usually declivous, usually armed; anterior coxae contiguous; antennal club obliquely truncate or with sutures on posterior face strongly displaced toward apex (rarely with sutures obsolete) 21

21(20). Eye shallowly sinuate (shallowly emarginate in some *Acanthotomicus*), its lower half distinctly narrower than above; protibia with 3-4 socketed teeth; antennal club rarely obliquely truncate (*Pityokteines*, *Orthotomicus*); procoxae contiguous, intercoxal piece longitudinally emarginate to absent, never complete; elytra moderately sulcate to elaborately excavated, with lateral margin usually armed by tubercles or spines; pronotum more strongly declivous on anterior third, asperities usually larger; worldwide .... **Ipini**

— Eye sharply, rather deeply emarginate (sinuate in *Deropria*), lower half usually almost equal in width to upper half; protibiae usually with four or more socketed teeth (most exceptions with lateral margins of pronotum acutely elevated); procoxae either contiguous or distinctly, narrowly separated; elytral declivity flattened to convex, unarmed by spines or large tubercles; pronotum either evenly arched from base to anterior margin or less strongly declivous on anterior third, asperities, when present, usually fine and abundant (a few exceptions) 22

22(21). Antennal funicle 4- to 6-segmented, club either obliquely truncate or with sutures on posterior face strongly displaced toward apex; anterior half of pronotum more strongly declivous and rather coarsely asperate (unarmed in *Tiarophorus*); worldwide ...... **Dryocoetini**

— Antennal funicle 2- or 3-segmented, club with sutures on posterior face about equal to those on anterior face; pronotum feebly declivous on anterior half and unarmed (minutely granulate in some *Aphanarthrum*), reticulate in many species; size small; Northern Hemisphere and Africa .... **Crypturgini**

23(19). Eye always completely divided into two parts; antennal funicle 4-segmented, base of club feebly to moderately corneous, usually pubescent to base; male subequal in size to female, his frons flattened or excavated and anterior margin of his pronotum more broadly rounded; male joins female in parental gallery, reproduction always bisexual; Holarctic and Oriental .... **Xyloterini**

— Eye emarginate except divided in some *Amasa*; funicle 5-segmented (3- or 4-segmented in a few Asiatic forms); males flightless, dwarfed, deformed, anterior slope of pronotum variously excavated; male head convex; male absent from parental gallery except as progeny; partly parthenogenetic, male haploid; almost worldwide .... **Xyleborini**

24(13). Costal margin of elytra slightly to moderately ascending from base of declivity to apex; basal end of metepisternum armed by a callus or partial groove of degenerating metepisternal spine (Fig. 31); sutures on posterior face of antennal club more strongly displaced toward apex; funicle 3- to 5-segmented; tibiae more strongly flattened, usually armed by more than four denticles; vestiture commonly includes scales; eye usually entire, less commonly emarginate; worldwide ..... **Cryphalini**

— Costal margin of elytra descending toward apex (except *Brachyspartus*); basal end of metepisternum with a small, transverse groove (Fig. 32) (concealed when elytra in locked position), elytra in locked position more completely cover metepisternum (Fig. 52 part 5, and 53); sutures on posterior face of antennal club only slightly displaced toward apex; funicle 1- to 5-segmented; tibiae more slender, rarely armed by more than four socketed denticles; vestiture rarely includes scales (in tropical forms only); eye emarginate; almost worldwide except Australia .... **Corthylini**

Subfamily Hylesininae

Hylesinen Erichson [1836:46, Type-genus: *Hylesinus* Fabricius, 1801]

Most previous classifications have recognized the Hylesininae as a major division of the taxon treated here as Scolytidae; however, there has been variability in the taxonomic rank assigned to it. Most of the distinguishing characters employed previously are not found consistently throughout the group and, consequently, have little or no taxonomic value.

The most consistent and reliable character available for the recognition of this subfamily is the procurved basal margins of the elytra that are armed by a row of crenulations, and the scutellar notch between them. The heavier, more coarsely armed tibiae are distinctive but less reliable as a distinguishing feature. The more primitive Bothrosternini, Diamerini, and a few other isolated examples lack the specialized elytral crenulations and have the basal margins elevated along a continuous costa reminiscent of some Platypodidae. This same character also occurs in *Dendrodicticus* (Carphodicticini) and, in a greatly reduced form, many Scolytini, Ctenophorini, and Cryphalini. On the other hand, a few *Cnemonyx* (allies of *galeritus*, Scolytini) have fully formed basal crenulations that suggest an affinity with the Hylesininae. Even though the demarcation between subfamilies is not as sharp as some would like, the division of subfamilies is simple and the characters are reliable.

Tribe Hylastini

Hylastes LeConte [1876:387, Type-genus: *Hylastes* Erichson, 1836]

DESCRIPTION.—Frons not sexually dimorphic; eye oval, entire; antennal scape elongate, funicle 7-segmented; precoxal ridge on prothorax strongly, acutely elevated; protibia very broad, with rather numerous lateral socketed teeth; scutellum visible; crenulations at base of elytra poorly developed, usually not forming a definite row; declivital interstriae 10 sometimes present (*Scierus*); declivital sculpture usually simple; vestiture usually includes scales (some exceptions); scutoscutellar suture parallel to costa of scutellar groove for two-thirds length of pronotum; metapleural suture descending subvertically from pleural wing process to metepisternal groove (this groove interlocking with groove on costal margin of elytron) then continuing caudad along this groove to a point near pleural coxal process; tarsal segment 3 wider than 1 or 2.

BIOLOGY.—All species are monogamous. They breed in coniferous hosts, usually at the base or in the roots of large trees, although some species prefer the lower surface of prostrate logs that are in contact with the ground. Parental galleries are monoramous or biramous, usually entirely in the phloem, but exposed on peeled bark. Eggs are placed in niches and are sealed in with frass. Larval mines are comparatively long and wander irregularly in the phloem. The species are not agressive, usually preferring unthirfty or felled trees after they have been attacked by other bark beetle species, except a few species of *Hylastes* have been reported to kill seedlings in nursery stock. Their role in the primary destruction of roots is unstudied.

TAXONOMY.—Members of this tribe are the most common fossil Scolytidae in Baltic amber (Oligocene). They are not always clearly separable from the Hylesinini to which they are obviously closely related phylogenetically, and they appear to be of ancient origin in the family. Their specialized habits apparently have resulted in evolutionary parallelism and superficial similarity of appearance with certain Cossoninae (Curculionidae), resulting in an erroneous supposition that the two groups are closely related. The generic limits within the Hylastini are not sharp. Individual variation within species and the similarity of species within genera make specific identification in the group rather difficult. They are strictly holarctic in distribution, if introductions to southern Africa, New Zealand, and Australia are ignored, and they are confined to the Pinaceae.

Key to the Genera of Hylastini

1. Anterior coxae rather widely separated by an intercoxal piece, its width at least equal to half width of a coxa; striae 9 and 10 both independently continued at least to level of abdominal sternum 4; elytral vestiture sparse, recumbent, yellow, hair- or bristlelike, never including scales; general surface of elytra and pronotum rather dull; body color reddish brown; North America; *Picea*, *Abies*, *Pinus*; 2.7-4.3 mm .... ***Scierus***

— Anterior coxae contiguous or at most with intercoxal piece narrower than one-fourth width of a coxa; striae 10 obsolete behind level of posterior coxae, only striae 9 continuing caudad; elytral vestiture longer, more abundant, usually including at least some small scales 2

Fig. 33. *Hylastes macer* LeConte, dorsal aspect (After Bright 1976: 206).

2(1). Third tarsal segments broad, bilobed; pronotum usually constricted anteriorly, usually about equal numbers of small and large punctures intermixed on disc; North America, N Africa, Europe, Asia; *Abies*, *Cedrus*, *Pinus*; 3.3-5.7 mm .... ***Hylurgops***

— Third tarsal segments narrower, emarginate; pronotum not noticeably constricted anteriorly (Fig. 33), punctures uniformly large or small, rarely intermixed with a few smaller ones; North America, N Africa, Europe, Asia, Canary Islands; *Abies*, *Cedrus*, *Picea*, *Pinus*; 2.0-5.5 mm .... ***Hylastes***

***Scierus* LeConte** [1876:390, Type-species: *Scierus annectens* LeConte, monobasic]. Distribution: 2 species in N and W North America where *Picea* grows. Both are monogamous and breed in phloem of roots, butts, and stumps of standing trees or next to the ground in the lower bole of prostrate trees. Keys: Bright (1976:41), Wood (1982:79).

***Hylurgops* LeConte** [1876:389, Type-species: *Hylastes pinifex* Fitch =*Hylurgops rugi-*

pennis pinifex (Fitch), subsequent designation by Hopkins 1914:123. Synonyms: *Hylesinites* Germar 1813:15, Type-species: *Hylesinites electrinus* Germar, monobasic; *Hylastites* Hagedorn 1907:117, Type-species: *Hylastites schellwieni* Hagedorn, monobasic; *Myelophilites* Hagedorn 1907:118, Type-species: *Myelophilites dubius* Hagedorn, monobasic; *Hylescierites* Schedl 1947:29, Type-species: *Hylescierites granulatus* Schedl, monobasic]. Distribution: 7 species, 2 with subspecies, in North America; 2 in N Africa; 18 nominate species in Europe and N Asia; 7 nominate fossil species including 1 from North America and 6 in Baltic amber (Oligocene). All are monogamous and breed in phloem tissues of Pinaceae; most are in roots, butts, and stumps of standing hosts, some in logs, and at least one may occur in smaller material. Keys: Wood (1982:82) for North America, Pfeffer (1944) for Europe and N Africa, Tsai and Huang (1964b) for China, Murayama (1963) for NE Asia.

***Hylastes* Erichson** [1836:47, Type-species: *Bostrichus ater* Paykull, subsequent designation by Westwood 1838:39 and Thomson 1859:146]. Distribution: 16 species in North America; 1 in Jamaica; 17 nominate species in Europe and N Asia; 1 in N Africa; 1 in the Canary Islands; fossil species include 2 from Baltic amber (Oligocene), 1 from Miocene of Colorado. All are monogamous and breed in phloem tissues of Pinaceae; most are in roots, butts, and stumps of standing trees, a few in the bole of prostrate trees next to the ground; seedlings are sometimes infested, apparently under emergency stress, for the purpose of maturation feeding or to wait for a suitable host. Keys: Wood (1982:93), and Blackman (1941) for North America, Pfeffer (1944) for Europe, Murayama (1963) and Tsai and Huang (1964a) for NE Asia.

Tribe Hylesinini

Hylesinen Erichson [1836:46, Type-genus: *Hylesinus* Fabricius, 1801]

Phloeotrupides Chapuis [1866:357, Type-genus: *Phloeotrupes* Erichson, 1836 =*Phloeoborus* Erichson, 1836]

Phloeobori Blandford [1893:426, Type-genus: *Phloeoborus* Erichson, 1836]

Dactylipalpi Blandford [1893:426, Type-genus: *Dactylipalpus* Chapuis, 1869]

Hylastinides Nüsslin [1912b:273, Type-genus: *Hylastinus* Bedel, 1888]

Alniphagini Murayama [1963:iii, 29, Type-genus: *Alniphagus* Swaine, 1918]

DESCRIPTION.—Frons obscurely to deeply and extensively impressed in male, female flat to variously convex; eye oval to elongate, entire to feebly sinuate on anterior margin; antennal scape very short to very elongate, funicle 6- or 7-segmented (except 5- to 7-segmented in *Hylesinopsis*), club conical to moderately flattened, symmetrical or nearly so, two or more sutures indicated, except sutures absent in *Dactylipalpus*; procoxae narrowly to moderately separated, precoxal ridge on prothorax moderately to very strongly, acutely elevated; pronotum armed by a few asperities, except absent in *Hylastinus*; metascutellar area separated from postnotum by a distinct suture; mesal surface of sutural groove of elytra just behind scutellum interrupted by a series of interlocking nodules and cavities; tarsal segment 3 usually wider than 2, often bilobed.

BIOLOGY.—All species are monogamous. All are phloeophagous except the xylophagous *Phloeoborus* and *Dactylipalpus*. Parental galleries are biramous or, if a well-developed turning niche is present, they may be monoramous. Eggs are deposited in niches and are sealed in with frass. Larval mines usually follow a definite course away from the parental mine and rarely cross one another. *Phloeoborus* and *Dactylipalpus* appear to have a symbiotic relationship with fungi, but not in a mycetophagous sense (old parental mines are stained black and wood adjacent to larval mines is discolored and in a more advanced state of decay).

TAXONOMY.—The occurrence of this tribe in the Eocene and its almost worldwide distribution suggest an ancient origin. The strictly neotropical *Phloeoborus* and ethiopian (except for two oriental species) *Dactylipalpus* suggest that these unique but related genera were derived from a common ancestral African stock at or before the time of separation of South America and Africa. The remaining American Hylesinini include representatives of *Hylesinus* and *Alniphagus*, both of which occur in Asia and appear to have reached North America in comparatively recent time. The one *Hylesinus* in South America (*antipodius* Schedl) is quite similar to living Australian species and was apparently

derived from Australian stock anciently. This suggests that *Hylesinus* is very old.

The African genera *Hylesinopsis* and *Rhopalopselion* appear to be comparatively young, and they are now going through a period of rapid evolutionary change. It could easily be argued that they should be grouped into a single genus and also that both should be fragmented into many small genera. However, it appears that only a small fraction of the African species have been discovered. It is anticipated that when more species are known most of the apparent character gaps will have disappeared, leaving only two major clusters of species.

Hylesinus and *Ficicis* have been grouped into one genus by most workers. However, when all species are examined, it is apparent that two distinct clusters of species are formed on both anatomical and biological (host choice) bases. Since these two cannot be combined without also including a third cluster of species (*Alniphagus*), I have elected to recognize all three as genera. *Alniphagus* appears to be more nearly allied to *Ficicis* than to *Hylesinus*.

The three clusters of genera mentioned above, together with the comparatively unrelated *Hylastinus*, *Kissophagus*, *Pteleobius*, *Cryptocurus*, and *Neopteleobius*, appear to represent remnants of a previous phyletic radiation that took place anciently. Although they cluster conveniently into one tribe, the extinction of intermediate forms makes comments on phylogenetic relationships difficult at this time.

Key to the Genera of Hylesinini

1. Antennal club subconical to strongly flattened, with three sutures clearly indicated, funicle 6- or 7-segmented (5-segmented in some *Hylesinopsis*); posterior face of protibia flattened to weakly convex, smooth, punctures with their lateral margins feebly or not at all tuberculate, lateral margin armed by socketed teeth; female pronotum never with a visible mycetangium; smaller, phloeophagous species, rarely larger than 5.0 mm 2

— Antennal club conical, either without sutures or with sutures 1 and 2 rather weakly indicated, funicle 7-segmented; posterior face of protibia moderately to strongly convex, rather coarsely, closely tuberculate, lateral margin without socketed teeth; female pronotum or propleuron with a conspicuous mycetangium; larger, xylophagous, tropical species, 5.0-16.0 mm 11

2(1). Antennal club subconical, elongate, at least 1.5 times as long as wide, sutures straight to feebly procurved; eye shorter, less than 3.0 times as long as wide (3.3 in *Hylastinus*); interstriae 10 never represented on posterior third of elytral length; body usually more slender 3

— Antennal club rather strongly flattened, stouter, less than 1.5 times as long as wide, sutures weakly to rather strongly procurved (if almost straight, then scutellum not visible), some species appear to have four or more sutures; eye elongate, at least 4.0 times as long as wide; interstriae 10 often narrowed and carinate on posterior third of elytra; body usually stouter; Africa 10

3(2). Frons convex in both sexes, not sexually dimorphic, sometimes marked by a fine, median carina; antennal funicle 6-segmented (except 7-segmented in *Hylastinus* which lacks pronotal asperities) 4

— Male frons moderately to very strongly impressed, female frons convex (or impressed in *Neopteleobius*), median carina absent or poorly represented; antennal funicle 7-segmented (except 6-segmented in *Neopteleobius*); pronotal asperities always present 6

4(3). Frontal rectangle (Fig. 1) conspicuously longer than wide; pronotum unarmed by asperities; antennal funicle 7-segmented; elytral ground vestiture of short, rather stout hair (not subplumose); Europe to W Asia, introduced almost worldwide; herbaceous to shrubby legumes; 2.0-2.5 mm . . . . ***Hylastinus***

— Frontal rectangle conspicuously wider than long; pronotum armed on anterolateral areas by a few fine asperities; antennal funicle 6-segmented; elytral ground vestiture of either plumose or scalelike setae 5

5(4). Frons with a fine, long, median carina; elytral ground vestiture of abundant, short, plumose setae of uniform color; pronotum more slender, 0.95 times as long as wide; Europe, N Africa, W Asia; *Hedra*; 2.0-2.2 mm . ***Kissophagus***

— Frons without a carina; elytral ground vestiture of abundant scales, their margins entire, usually forming patterns of light and dark color; pronotum stouter, less than 0.85 times as long as wide; Europe, N Africa, W Asia; *Ulmus*, *Sorbus*, etc.; 1.8-2.2 mm . . . . ***Pteleobius***

6(3). Male frons very strongly, extensively excavated to well above upper level of eyes; male declivity truncate and armed above and below by large, blunt processes; apical segments of male funicle each ornamented by one or more very long, coarse setae; Africa (Nigeria to Tanganyika); *Piptadenia*; 2.3-2.5 mm . . ***Cryptocurus***

— Male frontal impression less profound, rarely extending above eyes; declivity convex, one or more interstriae sometimes elevated and armed by smaller tubercles 7

7(6). Funicle 6-segmented; male and female frons impressed, strongly in male, moderately in fe-

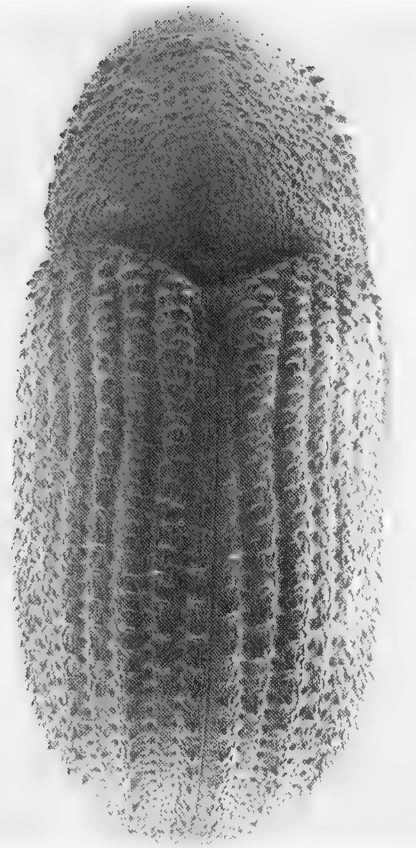


Fig. 34. *Alniphagus aspericollis* (LeConte), dorsal aspect (After Bright 1976: 207).

male, impression not extending above upper level of eyes; eye shallowly emarginate, elytral ground vestiture scalelike, costal margin near apex descending; E Asia; 2.2-2.8 mm . . . . ***Neopteleobius***

— Funicle 7-segmented; female frons flat to convex; male frons, if strongly concave, with excavation extending above eyes; eye less strongly to not emarginate 8

8(7). Eye entire, oval, less than 3.0 times as long as wide; protibia armed on lateral margin of apical fourth by six or more closely set, socketed teeth; body stouter; declivity more gradual, abdomen distinctly ascending to meet elytral apex; elytral vestiture of uniform length, mostly of scales (except almost subglabrous in *crenatus*); almost worldwide; *Fraxinus* and other Oleaceae; 1.7-4.8 mm . . . . ***Hylesinus***

— Eye shallowly emarginate, somewhat elongate, at least 3.3 times as long as wide; protibia armed by 2-5 socketed teeth; body more slender; declivity shorter, more abrupt, abdomen horizontal, not rising to meet elytral apex; elytral vestiture of ground cover of short hair or scales, and interstrial rows of longer, erect bristles 9

9(8). Male frons weakly, very shallowly impressed; protibia armed by five socketed teeth, outer apical angle only moderately abrupt; antennal club more nearly subconical; setae in elytral ground vestiture subplumose; Japan to W North America (Fig. 34); *Alnus*; 2.1-3.4 mm . . . . ***Alniphagus***

— Male frons moderately to extensively excavated; protibia armed by no more than four socketed teeth, outer apical angle abrupt; antennal club more strongly flattened, its apex less narrowly rounded; setae in elytral ground vestiture undivided, abundant to absent; Australia to Japan and China; *Ficus*, rarely other hosts; 1.6-5.0 mm . . . . ***Ficicis***

10(2). Pronotum subtriangular, scutellum small to absent; funicle 5-, 6-, or 7-segmented; striae often impressed, punctures usually larger; Africa; 1.3-3.0 mm . . . . ***Hylesinopsis***

— Pronotum subquadrate, scutellum rather large; funicle 6-segmented; striae usually weakly impressed, narrow, punctures fine to obsolete; Africa; 1.5-4.5 mm . . . ***Rhopalopselion***

11(1). Antennal club with two sutures (often obscure); female proepisternum with a large mycetangium ornamented by hair; metatarsus retractible into tibial groove; Central and South America; 5.0-16.0 mm . . . . ***Phloeoborus***

— Antennal club unmarked by sutures; female pronotum with a median, transverse, slitlike mycetangium on anterior third; metatarsus not retractible, tibial groove absent; Africa, SE Asia, Philippines; 6.0-14.0 mm . . . ***Dactylipalpus***

Hylastinus **Bedel** [1888:388, Type-species: *Ips obscurus* Marsham, original designation]. Distribution: 2 in Europe, 1 in N Africa; one of these (*obscurus*) has been introduced into most temperate areas of the world. One is phloeophagous in *Cytisus*; one (*obscurus*) breeds in the roots of various clovers. Keys: Reitter (1913:45).

Kissophagus **Chapuis** [1869:34, Type-species: *Hylesinus hederae* Schmitt, monobasic]. Distribution: 4 in Europe and neighboring areas. All are phloeophagous and monogamous. Key: Reitter (1913:44).

Pteleobius **Bedel** [1888:392, Type-species: *Bostrichus vittatus* Fabricius, subsequent designation by Hopkins 1914:128]. Distribution: 2 in Europe, one of these is recorded from N Africa. They are phloeophagous in *Ulmus* and *Sorbus* and are monogamous. Keys: Reitter (1913:42), Balachowsky (1949: 94).

***Cryptocurus* Schedl** [1957c:869, Type-species: *Cryptocurus spinipennis* Schedl, monobasic. Synonym: *Hyloperus* Browne 1970: 546, Type-species: *Hyloperus bicornis* Browne =*Cryptocurus spinipennis* Schedl, original designation]. Distribution: 1 in Africa (Nigeria to Tanganyika). It was attracted to light and was also taken from a *Piptadenia buchananii* log.

***Neoptelobius* Nobuchi** [1971:125, Type-species: *Hylesinus scutulatus* Blandford, original designation]. Distribution: 1 species in E Asia and Japan. Phloeophagous in several broadleaf hosts.

***Alniphagus* Swaine** [1918:73, Type-species: *Hylesinus aspericollis* LeConte, monobasic. Synonym: *Hylastinoides* Spessivitzev 1919:249, Type-species: *Hylastes alni* Niisima, monobasic]. Distribution: 2 in W North America, 1 in Japan and E Asia. All are phloeophagous in *Alnus* and are monogamous. Keys: Bright (1976:74) and Wood (1982:119) for North America.

***Hylesinus* Fabricius** [1801:390, Type-species: *Hylesinus crenatus* Fabricius, subsequent designation by Westwood 1838:39. Synonyms: *Leperisinus* Reitter 1913:41, Type-species: *Bostrichus fraxini* Panzer = *Bostrichus varius* Fabricius, subsequent designation by Swaine 1918:70]. Distribution: 10 in North America, 1 in South America, 5 in Europe, 9 in Asia, 1 in Africa (Uganda). More than 20 additional nominate species occur in S Asia, Australia, and neighboring areas. All are phloeophagous and are common in *Fraxinus* or other Oleaceae hosts; they are monogamous. Keys: Wood (1982:110) for North America, Murayama (1963:6) for NE Asia.

***Ficicis* Lea** [1910:147, Type-species: *Ficicis varians* Lea, subsequent designation by Hopkins 1914:122. Synonym: *Ficiphagus* Murayama 1958:930, Type-species: *Ficiphagus goliathoides* =*Hylesinus porcatus* Chapuis, original designation]. Distribution: About 16 nominate species in the area from India and Japan to Australia. All are monogamous and phloeophagous in *Ficus*, rarely in other hosts (particularly *Artocarpus*).

***Hylesinopsis* Eggers** [1920a:40, Type-species: *Hylesinopsis dubius* Eggers, monobasic. Synonyms: *Pseudohylesinus* Eggers 1919: 234, Type-species: *Pseudohylesinus togonus* Eggers, monobasic, preoccupied; *Metahylesinus* Eggers 1922:165, Type-species: *Pseudohylesinus togonus* Eggers, automatic; *Pseudophloeotribus* Eggers 1933b:18, Type-species: *Pseudophloeotribus africanus* Eggers, monobasic; *Trypographus* Schedl 1950e:213, Type-species: *Trypographus joveri* Schedl, monobasic; *Chilodendron* Schedl 1953a:74, Type-species: *Chilodendron planicolle* Schedl, monobasic; *Glochicopterus* Schedl 1954b:75, Type-species: *Glochicopterus baphiae* Schedl, monobasic; *Hapalophloeus* Schedl 1966b:363, Type-species: *Metahylesinus brinckei* Schedl, original designation; *Hemihylesinus* Schedl 1967:224, Type-species: *Hemihylesinus endroedyi* Schedl, monobasic]. Distribution: About 38 species in Africa (Considerable synonymy is anticipated). Apparently all are phloeophagous and monogamous.

***Rhopalopselion* Hagedorn** [1909:740, Type-species: *Rhopalopselion bituberculatum* Hagedorn, monobasic. Synonym: *Hapalogenius* Hagedorn 1912:352, Type-species: *Hapalogenius globosus* Hagedorn, monobasic]. Distribution: About 30 African species. Apparently all are phloeophagous and monogamous.

***Phloeoborus* Erichson** [1836:54, Type-species: *Phloeoborus rudis* Erichson, subsequent designation by Hopkins 1914:126. Synonym: *Phloeotrupes* Erichson 1836:53, Type-species: *Phloeotrupes grandis* Erichson, subsequent designation by Hopkins 1914:127]. Distribution: About 24 species, S Mexico to N Argentina. All are xylophagous in rather large host material and are monogamous; they are occasionally attracted to light. They have an intimate association with fungi, but are not mycetophagous. Keys: Blandford (1897:150, Eggers (1942:267), Wood (1982:122).

***Dactylipalpus* Chapuis** [1869:12, Type-species: *Dactylipalpus transversus* Chapuis, subsequent designation by Hopkins 1914: 120. Synonyms: *Dactylopselaphus* Gemminger & Harold 1872:2678, Type-species: *Dactylipalpus transversus* Chapuis, automatic; *Ethadopselaphus* Blandford 1896:321, Type-species: *Ethadopselaphus cicatricosus* Blandford, original designation]. Distribution: 10 African and 2 Philippine and SE Asian species. Apparently xylophagous in large host material; occasionally attracted to light. Key: Eggers (1933c:200).

Tribe Tomicini

Tomicidae Thomson [1859: 145, Type-genus: *Tomicus* Latreille, 1802/3]

Hylurgini LeConte [1876: 373, Type-genus: *Hylurgus* Latreille, 1807]

Dendroctonides Nüsslin [1912b: 273, Type-genus: *Dendroctonus* Erichson, 1836]

Xylechinides Nüsslin [1912b: 273, Type-genus: *Xylechinus* Chapuis, 1869]

DESCRIPTION.—Frons very weakly to moderately sexually dimorphic, male usually impressed, female convex; eye oval to ovate, entire; antennal scape elongate, funicle 4- to 7-segmented, club symmetrical, feebly to moderately flattened, three sutures usually indicated; pronotum unarmed, except a few very small asperities sometimes present in *Xylechinosomus* and some *Xylechinus*; procoxae contiguous to moderately separated, precoxal lateral costa absent; metascutellar area separated from postnotum by a distinct suture; sutural groove on mesal surface of elytra continuing to base without a series of interlocking nodules and cavities; tibiae armed by socketed denticles.

BIOLOGY.—All species are monogamous; all are phloeophagous except for the xylophagous *Pachycotes* (and *Hylurgonotus*?). The parental galleries are usually biramous, except in *Dendroctonus*, *Hylurgus*, and some *Tomicus* they are monoramous. Those of *Sinophloeus*, *Hylurgonotus*, and *Pachycotes* are not known to me. The eggs are placed in niches and packed in frass except that some *Dendroctonus* have modified the niches into elongate grooves into which numerous eggs are packed in single or double rows. The larval mines usually show on the inner surface of peeled bark and are oriented in a direction away from the parental mine. Symbiotic relationships with fungi may occur in all genera, but they are adapted toward overcoming resistance of the host and are not of a mycetophagous type.

TAXONOMY.—The worldwide distribution of this diversified tribe suggests an ancient origin, although only one Tertiary fossil has been reported (*Xylechinus*, Oligocene). The most conspicuous division of the group is that presented in couplet 1 of the key, except that *Xylechinus* should be placed with the first group of genera. The Tomicini represent the most highly evolved segment of an evolutionary trend that began in the Hylastini, continued in the Hylesinini, and reached its greatest specialization in the Tomicini.

Two major clusters of genera appear within the tribe: first, the *Xylechinus* group of genera (*Xylechinus, Chaetoptelius, Xylechinosomus, Sinophloeus, Dendrotrupes, Hylurgopinus, Pseudoxylechinus*, and *Pseudohylesinus*) and, second, the *Dendroctonus* group of genera (*Hylurgus, Tomicus, Dendroctonus, Hylurdrectonus*, and *Pachyucotes*). The first group appears to have radiated in a wide variety of hosts from South America and Australia since the beginning of the Tertiary. The second group appears to have been associated anciently with *Araucaria* hosts and is sparsely, uniformly represented in major geographical areas, except for Africa, in modern *Araucaria* and other Pinaceae.

Key to the Genera of Tomicini

1\. Metepisternal setae scalelike or plumose; antennal funicle 7-segmented 2

— Metepisternal setae usually hairlike (bifid in one *Hylurgonotus* having a 6-segmented funicle, and scalelike in *Xylechinus* having a 5-segmented funicle); antennal funicle 4- to 7-segmented 8

2(1). Anterolateral areas of pronotum distinctly asperate (minute in India species); antennal club apparently with either two or four transverse sutures; male frons strongly impressed . 3

— Anterolateral areas of pronotum unarmed; antennal club with three sutures clearly marked; male frons impressed or not 4

3(2). Antennal club more strongly flattened, more slender, at least 2.0 times as long as wide, apparently with two sutures; frontal rectangle at least as wide as long (0.8-1.0 times); Europe and Asia to Australia and New Zealand; mostly in broadleaf hosts; 1.8-5.0 mm . . . . ***Chaetoptelius***

— Antennal club less strongly flattened, stouter, less than 1.5 times as long as wide, apparently with four sutures; frontal rectangle longer than wide (about 1.2 times); South America; *Araucaria*; 1.5-3.4 mm . . . . ***Xylechinosomus***

4(2). Male frons strongly impressed; median frontal carina present; pronotum either without a constriction affecting dorsal profile (*Sinophloeus*) or with a moderate lateral constriction on anterior third (*Dendrotrupes*) 5

— Male frons convex to modestly flattened, median carina present or absent; pronotum with a conspicuous transverse constriction on anterior third affecting dorsal profile 6

5(4). Antennal club elongate, 2.0 times as long as wide, apparently with four or five sutures;

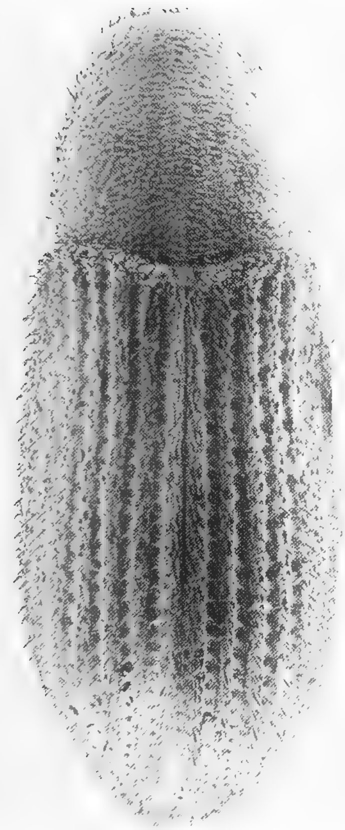


Fig. 35. *Xylechinus montanus* Blackman, dorsal aspect (After Bright 1976: 206.

declivital interstriae 2 impressed, 3 (sometimes 1-7) armed by rounded tubercles; pronotum conspicuously wider than long (0.7 times as long as wide); larger; South America; *Nothophagus*; 2.3-3.0 mm .... ***Sinophloeus***

— Antennal club more compact, less than 1.5 times as long as wide, with three sutures; declivity variable; pronotum almost as long as wide (0.9 times); New Zealand; hosts not coniferous; 1.5-2.0 mm .... ***Dendrotrupes***

6(4). Elytral vestiture hairlike, ground vestiture moderately stout; frontal carina absent; antennal club slightly flattened, segment 1 one-fourth of its length; North America; *Ulmus*; 2.0-2.5 mm .... ***Hylurgopinus***

— Vestiture of abundant, conspicuous scales (one exception with no ground setae); median frontal carina usually present; antennal club more conical 7

7(6). Strial punctures small, close; interstriae two or more times as wide as striae, unarmed (except coarsely tuberculate and without ground vestiture in *rugatus*), erect setae closer and coarser; elytral ground setae more slender and appically pointed, variegated patterns obscure; antennal club somewhat more flattened and apex less pointed; China; broadleaf hosts; 1.8-3.0 mm . ***Pseudoxylechinus***

— Strial punctures coarse; interstriae less than 1.5 times as wide as striae, often armed by tubercles of moderate size; elytral ground setae usually stout, apically rounded, and forming conspicuous variegated patterns; antennal club more nearly conical, segment 1 usually conspicuously longer; North America; coniferous hosts; 2.2-5.8 mm ..... ***Pseudohylesinus***

8(1). Ground vestiture on elytra scalelike, metepisternal setae scalelike (Fig. 35); antennal funicle 5-segmented; median frontal carina present (except absent in a few South American species); procoxae rather widely separated; North and South America, Europe, Asia, Africa, Australia; coniferous and broadleaf hosts; 1.5-3.5 mm .... ***Xylechinus***

— Ground vestiture on elytral disc hairlike, metepisternal setae hairlike (except some *Hylurgonotus*, female *Hylurdrectonus*) 9

9(8). Protibiae armed by five or more socketed teeth on distal and lateral margins; male frons convex except in *Hylurdrectonus*; phloeophagous 10

— Protibiae armed by three socketed teeth (four in two *Hylurgonotus*) on distal margin; male frons feebly to strongly, extensively excavated; xylophagous in *Araucaria* 13

10(9). Antennal funicle 6-segmented, club conical . 11

— Antennal funicle 5-segmented, club moderately flat 12

11(10). Procoxae contiguous; pronotum more slender, 0.95-1.1 times as long as wide, only slightly constricted on anterior thrid; erect interstrial setae abundant, confused; a short median carina from epistomal margin to level of antennal insertion; Europe, W Asia; *Pinus*; 3.1-5.3 .... ***Hylurgus***

— Procoxae moderately separated; pronotum stouter, less than 0.85 times as long as wide, strongly constricted on anterior third; erect interstrial setae in uniseriate rows (except confused in *puellus*); a fine median carina from epistoma to middle of frons (absent in *puellus*); Europe, Asia, N Africa; 2.5-4.5 mm .... ***Tomicus***

12(10). Antennal club with sutures somewhat procurved; procoxae contiguous; male frons convex to weakly impressed; vestiture never scalelike in either sex; North America, Europe, Asia; *Pinus, Picea, Larix, Pseudotsuga*; 2.5-9.0 mm .... ***Dendroctonus***

— Antennal club with sutures straight, transverse; procoxae moderately separated; male frons rather strongly concave; female elytra with some scales (except *araucariae*); Australia, New Guinea; *Araucaria*; 1.3-1.8 mm .... ***Hylurdrectonus***

13(9). Declivital vestiture hairlike (except scalelike in *tuberculatus*); protibiae with either three or four socketed teeth; male frons rather shallowly impressed (except deeper in *antipodius*); South America; *Araucaria*; 2.7-4.6 mm .... ***Hylurgonotus***

— Declivital vestiture always includes scales (sparse in male *peregrinus*); protibiae with three socketed teeth; male frons strongly, more extensively impressed (except weak in *peregrinus*); Australia, New Zealand, and adjacent islands; *Araucaria*; xylophagous; 2.3-4.5 mm .... ***Pachycotes***

Chaetoptelius **Fuchs** [*in* Reitter 1913: 43, Type-species: *Hylesinus vestitus* Mulsant & Rey, automatic. Synonyms: *Homarus* Broun 1881: 740, Type-species: *Homarus mundulus* Broun, automatic, preoccupied; *Acrantus* Broun 1882: 409, Type-species: *Homorus mundulus* Broun, automatic, preoccupied; *Chaetophorus* Fuchs 1912: 46, Type-species: *Hylesinus vestitus* Mulsant & Rey, monobasic, preoccupied]. Distribution: 1 species in Europe and W Asia, 1 in New Zealand, about 8 in Australia and New Guinea. All are phloeophagous and monogamous.

Xylechinosomus **Schedl** [1963a: 209, Type-species: *Xylechinus taunayi* Eggers, original designation]. Distribution: About 9 species in South America. All are phloeophagous in *Araucaria*.

Sinophloeus **Brèthes** [1922b: 433, Type-species: *Sinophloeus porteri* Brèthes, monobasic]. Distribution: 2 species in South America. Apparently phloeophagous in *Nothofagus*.

Dendrotrupes **Broun** [1881: 741, Type-species: *Dendrotrupes costiceps* Broun =*Dendrotrupes vestitus* Broun, subsequent designation by Hopkins 1914: 120]. Distribution: 3 species in New Zealand. Phloeophagous.

Hylurgopinus **Swaine** [1918: 43, 74, Type-species: *Hylastes rufipes* Eichhoff, original designation]. Distribution: 1 species in North America. Phloeophagous in *Ulmus* and monogamous.

Pseudoxylechinus **Wood & Huang** [1986: 465, Type-species: *Pseudoxylechinus uniformis* Wood & Hwang, original designation]. Distribution: 7 species in Asia. All are phloeophagous and monogamous in broadleaf trees.

Pseudohylesinus **Swaine** [1917: 11, Type-species: *Pseudohylesinus grandis* Swaine =*Hylurgus sericeus* Mannerheim, original designation]. Distribution: 11 species in North America. Phloeophagous in *Abies*, *Picea*, *Pinus*, *Pseudotsuga*, and *Tsuga* and monogamous. Keys: Blackman (1942a: 5), Bright (1969: 15), Wood (1982: 130).

Xylechinus **Chapuis** [1869: 36, Type-species: *Hylesinus* (*Dendroctonus*) *pilosus* Ratzeburg, monobasic. Synonyms: *Pruniphagus* Murayama 1958: 930, Type-species: *Pruniphagus gummensis* Murayama, original designation; *Squamasinulus* Nunberg 1964: 431, Type-species: *Squamasinulus chiliensis* Nunberg, original designation; *Xylechinops* Browne 1973: 283, Type-species: *Xylechinus australis* Schedl, original designation]. Distribution: 19 species in Central and South America, 2 in North America, 2 in Africa, 5 in Asia, and 1 in Europe. All are phloeophagous and monogamous. Keys: Blandford (1897: 157), Wood (1982: 143) for North and Central America.

Hylurgus **Latreille** [1807: 274, Type-species: *Hylesinus ligniperda* Fabricius, monobasic]. Distribution: 3 species in Europe, W Asia, N Africa. All are phloeophagous in coniferous hosts and monogamous.

Tomicus **Latreille** [1802/3: 203, Type-species: *Hylesinus piniperda* Fabricius =*Dermestes piniperda* Linnaeus, monobasic. Synonyms: *Blastophagus* Eichhoff 1864: 25, Type-species: *Dermestes piniperda* Linnaeus, preoccupied, subsequent designation by Lacordaire 1866: 360; *Myelophilus* Eichhoff 1878c: 400, Type-species: *Dermestes piniperda* Linnaeus, automatic]. Distribution: 8 species in Europe and Asia. All are phloeophagous in *Pinus* and are monogamous. Keys: Murayama (1963: 35) for the Far East, Balachowsky (1949: 135) for France, Schedl (1946b: 52) for the genus.

Dendroctonus **Erichson** [1836: 52, Type-species: *Bostrichus micans* Kugelann, subsequent fixation by International Commission on Zoological Nomenclature 1974: 230]. Distribution: 16 species in North America and 2 in Eurasia. All are phloeophagous in *Pinus*, *Picea*, *Larix*, and *Pseudotsuga* and are monogamous. Keys: Hopkins (1909: 69), Wood (1963: 26, 1982: 151).

Hylurdrectonus **Schedl** [1938b: 40, Type-species: *Hylurdrectonus piniarius* Schedl, monobasic. Synonym: *Xylogopinus* Schedl 1972: 64, Type-species: *Xylogopinus araucar-*

iae Schedl =*Hylurdrectonus corticinus* Wood, monobasic]. Distribution: 3 species in Australia and New Guinea. Phloeophagous in *Araucaria* except one in central axis of leaflet; monogamous.

***Hylurgonotus* Schedl** [1951e: 448, Type-species: *Hylurgonotus brunneus* Schedl =*Hylurgus tuberculatus* Eggers]. Distribution: 4 species in South America. In *Araucaria*, possibly xylophagous and apparently monogamous.

***Pachycotes* Sharp** [1877: 10, Type-species: *Pacycotes ventralis* Sharp =*Hylesinus peregrinus* Chapuis, monobasic]. Distribution: 8 species in Australia, New Zealand, and New Guinea. All are xylophagous in logs and monogamous.

Tribe Phrixosomini

Phrixosomini Wood [1978: 111, Type-genus: *Phrixosoma* Blandford, 1897]

DESCRIPTION.—Frons not sexually dimorphic, frequently with a fine, median carina; eye completely divided; antennal scape elongate, funicle 6-segmented, club rather strongly flattened, slightly asymmetrical, unmarked by sutures, except 1 partly septate; pronotum unarmed by asperities, procoxae contiguous; scutoscutellar suture remote from scutellar groove, postnotum separated from scutoscutellar area of metanotum by a complete suture; tibiae armed on lateral margin by socketed denticles.

BIOLOGY.—These monogamous, phloeophagous, tropical species are restricted to hosts of the Guttiferae. The parental galleries are usually biramous, although a third egg tunnel is not uncommon, with the galleries either longitudinal, transverse, or without definite orientation. The eggs are deposited in niches and sealed in by frass. The larval mines show on the inner surface of peeled bark, but they are almost entirely in the bark and usually wander indiscriminantly without respect to the grain of the wood.

TAXONOMY.—Only one genus is known (Fig. 36). It is apparently very old and represents a group that is otherwise extinct. They are unknown in the fossil record. The one genus in South America and Africa in Guttiferae has changed so little since separation of these land masses that division into species groups is not recommended. Although more closely allied to Hylesinini than to other tribes, this genus is quite unique.

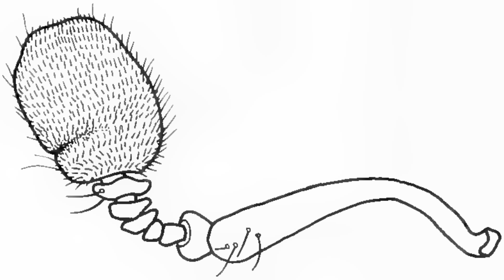


Fig. 36. *Phrixosoma magna* Blackman, antenna.

***Phrixosoma* Blandford** [1897: 148, Type-species: *Phrixosoma rude* Blandford, monobasic. Synonyms: *Bothryperus* Hagedorn 1909: 742, Type-species: *Bothryperus psaltes* Hagedorn, monobasic; *Neohylesinus* Eggers 1920b: 118, Type-species: *Neohylesinus quadrioculatus* Eggers, monobasic; *Sphaerosinus* Eggers 1929: 40, Type-species: *Sphaerosinus striatus* Eggers, monobasic]. Distribution: 13 species in Central and South America and 9 in Africa. All are phloeophagous in Guttiferae and are monogamous. Key: Wood (1982: 204).

Tribe Hyorrhynchini

Hyorrhynchinae Hopkins [1915b: 225, Type-genus: *Hyorrhynchus* Blandford, 1894]

Sueinae Murayama [1958: 7, Type-genus: *Sueus* Murayama, 1951]

DESCRIPTION.—Frons sexually dimorphic, male slightly to strongly impressed, female convex; eye completely divided; antennal scape either long or short, funicle 5- or 6-segmented, club aseptate and either unmarked by sutures or with two sutures; pronotum armed or not; procoxae moderately to widely separated, precoxal ridge obsolete; scutoscutellar suture remote from scutellar groove; scutoscutellar area separated from postnotum by a distinct suture; tibiae without socketed denticles.

BIOLOGY.—The species are myelomycetophagous or xylomycetophagous and form simple, monoramous tunnels in the pith or xylem of twigs or small branches. Only two larvae were seen (*Sueus niisimai*) and these were in the parental chamber. Males of *Sueus* are very rare, dwarfed, and deformed; reproduction in this genus is apparently by

arrhenotocous parthenogenesis. In *Hyorrhynchus* and *Pseudohyorrhynchus* the males are similar in size, shape, and abundance to the females, suggesting a normal bisexual relationship.

TAXONOMY.—A dozen species assigned to three genera are listed in the literature. All occur in the area from India and Japan to New Guinea. They form an aberrant, relect group of uncertain affinity but are considered to be among the most primitive of the Hylesininae. Although definitely members of the Hylesininae, they share more primitive characters with primitive Scolytinae and Platypodidae than with other members of their own subfamily.

Key to the Genera of Hyorrhynchini

1. Antennal funicle 5-segmented, club rather weakly compressed; male dwarfed, rare, flightless; male frons convex, with median carina; tarsal segment 3 entire; Sri Lanka (Ceylon) and New Guinea to Japan; female 1.6-2.0 mm, male 1.0-1.3 mm .... ***Sueus***

— Antennal funicle 6- or 7-segmented, club rather strongly flattened; male subequal in size to female, shares parental gallery; male frons concave or not, with or without a carina; tarsal segment 3 emarginate to bilobed 2

2(1). Antennal funicle 6-segmented, club with two clearly marked sutures; male frons concave, without a carina; tarsal segment 3 emarginate; interstrial tubercles minute; India to Japan; 2.7-5.0 mm .... ***Hyorrhynchus***

— Antennal funicle 7-segmented, club without sutures; tarsal segment 3 deeply bilobbed; male frons not impressed, with a median carina; interstrial tubercles on declivity rather coarse; Japan; 3.5-3.6 mm .... ***Pseudohyorrhynchus***

Sueus **Murayama** [1951: 1, Type-species: *Sueus sphaerotrypoides* Murayama =*Hyorrhynchus niisimai* Eggers, original designation. Synonym: *Neohyorrhynchus* Schedl 1962e: 202, Type-species, *Hyorrhynchus niisimai* Eggers, original designation]. Distribution: 2 species from Sri Lanka (Ceylon) and New Guinea to Japan. Xylomycetophagous in small branches and, apparently, at least partly parthenogenetic (only one series of males known).

Hyorrhynchus **Blandford** [1894a: 58, Type-species: *Hyorrhynchus lewisi* Blandford, monobasic]. Distribution: About 10 species from India to Japan. Habits have not been reported except host species include *Acer*, *Fagus*, and *Macaranga*; the species are xylomycetophagous and monogamous (Nobuchi, pers. comm.).

Pseudohyorrhynchus **Murayama** [1950b: 61, Type-species: *Pseudohyorrhynchus wadai* Murayama, original designation]. Distribution: 1 species from Japan. Specimens of this monogamous species attack living *Cornus* twigs where they are xylomycetophagous.

Tribe Diamerini

Diameridae Hagedorn [1909: 734, Type-genus: *Diamerus* Erichson, 1836]
Strombophorini Schedl [1959e: 75, Type-genus: *Strombophorus* Hagedorn, 1909]
Sphaerotrypini Murayama [1963: 5, Type-genus: *Sphaerotrypes* Blandford, 1894]

DESCRIPTION.—Frons dimorphic, feebly to very strongly impressed in male, flattened to convex in female; eye entire to completely divided; antennal scape usually elongate, funicle 6- to 7-segmented, club flattened, sutures variable, one to several (five or more, mostly pseudosutures); procoxae moderately to widely separated; scutoscutellar suture remote from scutellar groove, postnotum fused to scutoscutellar area of metanotum, intersegmental suture obsolete on median half.

BIOLOGY.—These monogamous, phloeophagous species are largely restricted to tropical and subtropical areas of the eastern hemisphere. The parental galleries are mostly biramous and either longitudinal or transverse. The eggs are deposited in niches and sealed in by frass. The larval mines show on the inner surface of peeled bark and tend to radiate away from the parental tunnel without respect to the grain of the wood in most species; the latter parts of the tunnels in some species are parallel to the grain of wood.

TAXONOMY.—Seven genera represented by about 122 species occur in Africa and southeastern Asia to Australia. *Pseudodiamerus*, *Pernophorus*, and *Strombophorus* occur only in Africa. They appear to form a sister group derived from the same ancestral stock as Bothrosternini and, if this is the case, these groups have differentiated and radiated since early Tertiary. Features used to characterize this tribe vary and tend to intergrade with Phloeosinini. Although future study may require combination of these two tribes, their division gives a convenient break in a large and diverse group.

Key to the Genera of Diamerini

1. Eye oval, neither strongly reduced on lower half nor completely divided; antennal club with fewer than three sutures, funicle 5-, 6-, or 7-segmented 2

— Eye either strongly narrowed on lower half or entirely divided into two parts; antennal club apparently with five or more sutures marked by constrictions and/or rows of setae, funicle 6-segmented (except 7-segmented in *Pernophorus*) . 5

2(1). Costal margin on basal fourth of elytra normal, not emarginate, metepisternum not expanded; median anterior area of pronotum usually finely asperate; antennal funicle 6-segmented; club elongate, sutures 1 and 2 feebly indicated (straight) to absent; Africa, SE Asia to Australia; 1.1-2.5 mm . . . . *Acacicis*

— Costal margin on basal fourth of elytra either normal or deeply, abruptly emarginate, when emarginate metepisternum expanded into this emargination; pronotum never asperate (feeble lateral asperities in *Bothrosternoides*) 3

3(2). Costal margin on basal fourth of elytra deeply emarginate (Fig. 37); suture 1 on antennal club strongly, subangulately procurved; Africa, SE Asia to Australia; 3.0-5.0 mm . . . . *Diamerus*

— Costal margin on basal half of elytra almost normal, straight to weakly emarginate; basal margins of elytra either costate or armed by a row of coarse crenulations; protibia with two to four curved spines; male frons shallowly impressed; suture 1 on antennal club weakly indicated (straight) or absent 4

4(3). Eye more than 3 times as long as wide; funicle 7-segmented; club with suture 1 straight, feeble; protibia with two apical and two lateral spines; costal margin not emarginate; basal margins of elytra crenulate; pronotum without lateral granules; Africa (Angola); 2.2-3.0 mm . . . . *Pseudodiamerus*

— Eye twice as long as wide; funicle 5-segmented, club unmarked by sutures; protibia with two apical and one small posterior subapical spine and several lateral posterior granules; costal margin shallowly emarginate at base; basal margins of elytra strongly costate; some prothoracic granules or small asperities in lateral areas; male with median epistomal tubercle; body very stout; Malaya; 2.3 mm . . . . *Bothrosternoides*

5(1). Eye completely divided; scutellum visible, longer than wide; pronotum unarmed by asperities; body very stout, subglobular; Africa, SE Asia; 1.5-5.0 mm . . . . *Sphaerotrypes*

— Eye strongly constricted on lower half to about one-third width of upper half; pronotum at least partly asperate; scutellum not visible; body elongate-oval 6

6(5). Antennal funicle 7-segmented; elytral vestiture hairlike to subplumose; Africa; 4.0 mm . . . . *Pernophorus*

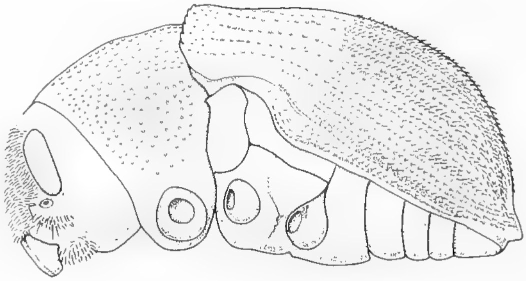


Fig. 37. *Diamerus curvifer* Walker, lateral aspect of female.

— Antennal funicle 6-segmented; elytral vestiture with ground cover scalelike; Africa; 1.5-3.5 mm . . . . *Strombophorus*

Acacacis **Lea** [1910: 149, Type-species: *Acacacis abundans* Lea, monobasic. Synonyms: *Trogloditica* Sampson 1922: 148, Type-species: *Trogloditica trahax* Sampson, monobasic; *Pseudoacacacis* Schedl 1963c: 477, Type-species: *Acacacis borneensis* Browne, original designation; *Neodiamerus* Schedl 1971b: 282, Type-species: *Neodiamerus granulicollis* Schedl, original designation]. Distribution: 5 species in Africa, 2 in Sri Lanka, 2 in Malaya, 1 in Borneo, 1 in New Guinea, and 2 in Australia. All are phloeophagous and monogamous.

Pseudodiamerus **Eggers** [1933b: 18, Type-species: *Pseudodiamerus striatus* Eggers, monobasic]. Distribution: 3 species in Africa. All are apparently phloeophagous and monogamous.

Bothrosternoides **Schedl** [1969: 210, Type-species: *Bothrosternoides malayensis* Schedl, monobasic]. Distribution: 1 species in Malaya. Three specimens intercepted in Japan and 4 in China in imported Nyatoh logs.

Diamerus **Erichson** [1836: 57, Type-species: *Hylesinus hispidus* Klug, monobasic. Synonyms: *Acanthurus* Eichhoff 1886: 24, Type-species: *Acanthurus spinipennis* Eichhoff = *Hylesinus curvifer* Walker, subsequent designation by Hopkins 1914: 116; *Lissoclastus* Schaufuss 1905: 71, Type-species: *Lissoclastus pimelioides* Schaufuss, monobasic]. Distribution: About 11 species in Africa and 28 in the Indo-Australian and Oriental areas. All are phloeophagous and monogamous.

Sphaerotrypes **Blandford** [1894a: 61, Type-species: *Sphaerotrypes pila* Blandford, subsequent designation by Hopkins 1914: 129. Syn-

onym: *Parasphaerotrypes* Murayama 1958: 933, Type-species: *Sphaerotrypes controversae* Murayama, original designation]. Distribution: 8 nominate species in Africa and about 35 in the Indo-Australian and Oriental areas.

Pernophorus **Strohmeyer** [1910b: 92, Type-species: *Acanthophorus brevicollis* Strohmeyer, automatic. Synonym: *Acanthophorus* Strohmeyer 1910a: 69, Type-species: *Acanthophorus brevicollis* Strohmeyer, monobasic, preoccupied]. Distribution: 5 nominate species in Africa. They are apparently phloeophagous and monogamous.

Strombophorus **Hagedorn** [1909: 740, Type-species: *Strombophorus crenatus* Hagedorn, subsequent designation by Hopkins 1914: 130]. Distribution: About 34 species in Africa. They are phloeophagous and monogamous.

Tribe Bothrosternini

Bothrosterni Blandford [1896a: 120, Type-genus: *Bothrosternus* Eichhoff, 1868]

DESCRIPTION.—Frons usually sexually dimorphic; eye entire to slightly sinuate; funicle 6-segmented, club symmetrical, moderately flattened, sutures indicated; procoxae moderately separated; protibia bearing a bifid process on outer apical angle exceeding inner apical angle; pronotum unarmed; crenulations on basal margins of elytra poorly developed, sometimes represented by a continuous costa; at least part of scutoscutellar suture parallel to margin of scutellar groove; postnotum fused to scutoscutellar area of metanotum, suture obsolete.

BIOLOGY.—All species are monogamous, except that a form of parthenogenesis probably exists in *Bothrosternus*. All are myelophagous, except that *Bothrosternus* and, possibly, *Eupagiocerus ater* Eggers are myelomycetophagous. In *Cnesinus annectens* Wood typical transverse, biramous egg galleries are formed in the cambium region of the host by parent beetles, complete with egg niches, and the larvae feed briefly in the cambium region before following the parent beetles to the pith region. Typically, the parental pith tunnel is biramous; the eggs are deposted in clusters in the loose frass in this cavity; and the larvae feed in congress while extending the parental pith tunnel. Pupation occurs in the larval frass.

TAXONOMY.—The tribe is restricted to the American tropics, with two species extending into the southern United States. It appears to be the New World counterpart of the closely allied Diamerini. The genera of Bothrosternini differ anatomically from one another only slightly and may be recognized with difficulty in some instances. The protibial and antennal structure and the costate basal margins of the elytra in at least some members suggest a very primitive position in classification. Though primitive as a group, modern representatives appear to have evolved since the beginning of the Tertiary to their present ecological and structural status, because clearly identifiable related groups are not known outside of the neotropical realm. They appear to be more nearly allied to Diamerini and Hyorrhynchini than to any American groups.

Key to the Genera of Bothrosternini

1. Lateral margins of pronotum rounded 2
— Lateral margins of pronotum marked by a sharply elevated, costate to subcostate line 3
2(1). Sutures of antennal club transverse, straight; rostrum distinctly wider than distance between eyes; pronotum either longitudinally strigose or punctured; pith borers of twigs and other small stems; SE USA to South America; 1.6-3.5 mm .... ***Cnesisnus***
— Sutures of antennal club strongly procurved; rostrum width at tip equal to distance between eyes; frons excavated in both sexes, with a median tubercle just above epistoma; body oval; seed borers; SE USA to South America, intercepted elsewhere in maize, etc.; 1.9-2.6 mm .. .. ***Pagiocerus***
3(1). Sutures of antennal club strongly procurved; pith borers in twigs and woody vines; Central and South America; 2.1-3.8 mm ... ***Eupagiocerus***
— Sutures of antennal club transverse, straight ... 4
4(3). Proepisternal area partly excavated, with cavity densely filled by yellow pubescence, particularly in female; prothoracic intercoxal piece with a transverse, subcarinate ridge; elytral interstriae usually not strongly carinate; ambrosia beetles in axial tunnels of woody vines; Central and South America; 1.9-3.3 mm .. ***Bothrosternus***
— Proepisternal area normal, not densely pubescent; prothoracic intercoxal ridge absent; elytral interstriae narrowly carinate from posterior part of disc to apex; pith borers in branches and twigs; Central and South America; 2.2-3.6 mm .... ***Sternobothrus***

Cnesinus **LeConte** [1868: 171, Type-species: *Cnesinus strigicollis* LeConte, monobasic. Synonym: *Nemophilus* Chapuis 1869: 27,

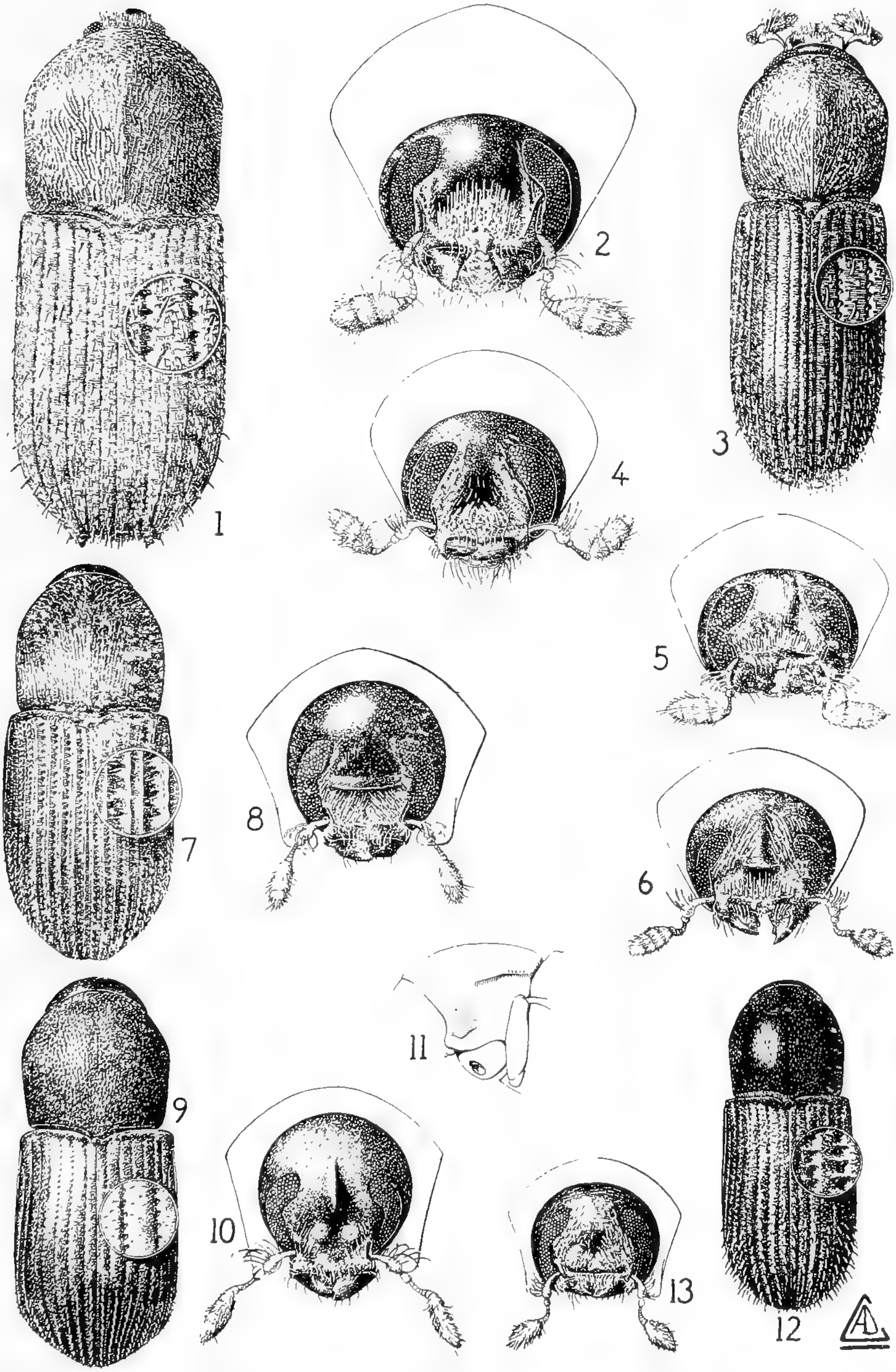


Fig. 38. Bothrosternini: 1-8, *Cnesinus* spp., (1) *cubensis* Blackman, dorsal aspect, (2) same, female head, (3) *panamensis* Blackman, dorsal aspect, (4) same, male head, (5) *robai* Blackman, male head, (6) *setulosus* Blandford, female head, (7) *costulatus* Blandford, dorsal aspect, (8) same, female head, (12) *blackmani* Schedl, dorsal aspect; 9-11, *Bothrosternus foveatus* Blackman, (9) dorsal aspect of female, (10) female head, (11) propleuron of female. (After Blackman 1943: pl. 15).

Type-species: *Nemophilus strigillatus* Chapuis =*Cnesinus strigicollis* LeConte, subsequent designation by Hopkins 1914: 125]. Distribution: About 101 species from the USA to Argentina. All are monogamous and myelophagous except that one is partly phloeophagous. Keys: Wood (1968b: 88, 1982: 209).

***Pagiocerus* Eichhoff** [1868a: 148, Type-species: *Pagiocerus rimosus* Eichhoff =*Bostrichus frontalis* Fabricius, subsequent designation by Hopkins 1914: 126]. Distribution: About 5 species are known from the USA to Argentina, 1 is occasionally intercepted worldwide in large seeds, including maize. All are monogamous and spermophagous.

***Eupagiocerus* Blandford** [1896d: 133, Type-species: *Eupagiocerus dentipes* Blandford, monobasic. Synonym: *Nemopagiocerus* Schedl 1962a: 85, Type-species: *Eupagiocerus nevermanni* Schedl =*Eupagiocerus ater* Eggers, monobasic]. Distribution: 4 species from Mexico (Chiapas) to Venezuela and Peru. All are monogamous and myelophagous in woody vines. Keys: Wood (1965: 31, 1982: 249).

***Bothrosternus* Eichhoff** [1868a: 150, Type-species: *Bothrosternus truncatus* Eichhoff, monobasic]. Distribution: About 12 species from Mexico (Veracruz) and Jamaica to Peru and Brazil. Monogamous and some species apparently with a type of parthenogenesis (involving consanguineous polygyny), and myelophagous in woody vines. Key: Wood (1982: 247).

***Sternobothrus* Eggers** [1943: 372, Type-species: *Bothrosternus cancellatus* Chapuis, original designation]. Distribution: About 10 species from Costa Rica to Bolivia and Brazil. Monogamous and myelophagous, three species breed in *Nectandra* branches. Key: Wood (1982: 254).

Tribe Phloeotribini

Phloeotribidae Chapuis [1869: 42, Type-genus: *Phloeotribus* Latreille, 1796]
Phthorophloeides Nüsslin [1912b: 273, Type-genus: *Phthorophloeus* Rey, 1883]

DESCRIPTION.—Frons sexually dimorphic, male variously impressed, female flat to convex; eye entire; funicle 5-segmented, club almost non-existent to strongly asymmetrical, deeply divided into three movable, sublammelate segments; procoxae contiguous; pronotum armed or not, its lateral margins rounded; metatergum fused to its postnotum.

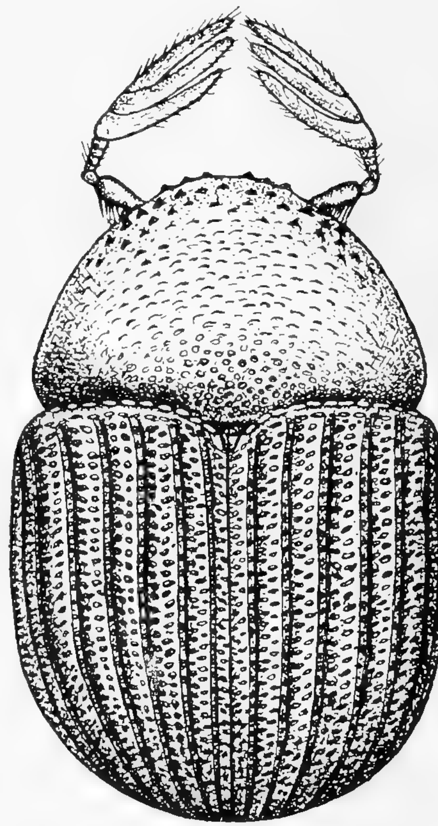


Fig. 39. *Phloeotribus pilula* Erichson, dorsal aspect of male. (After Schedl 1953: 80).

BIOLOGY.—All are monogamous and phloeophagous. Parental galleries are biramous and engrave the wood rather deeply. Eggs are deposited in niches packed in frass. Larval mines follow a rather definite course away from the parental tunnels and usually do not cross one another; in the latter stages they may engrave the wood rather deeply. A few species bore rather deeply into subsurface tissues of woody vines; one species breeds in the fruiting pods of its host (*Inga*).

TAXONOMY.—The tribe apparently originated in South America, where a majority of the species now occur. *Aricerus* and one very primitive *Phloeotribus* apparently reached Australia very early; much later a few species of *Phloeotribus* reached North America and then spread from there to northern Asia, Eu-

rope, and North Africa. The tribe apparently was derived from the same parental stock as the Phloeosinini, although the relationship is not close. The distribution, freely movable antennal club segments (Fig. 39), and the tibial structure of *Aricerus* and at least one species of *Phloeotribus* suggest an origin in early Tertiary or late Cretaceous while it was still possible to spread to Australia, but not into Africa. The one Australian and a few European *Phloeotribus* (Fig. 27) have virtually no club on the antenna, suggesting the possibility that the club of Scolytidae could have been derived independently from that of other curculionoids.

Key to the Genera of Phloeotribini

1. Lateral margin of protibia without socketed teeth, outer apical angle rather strongly produced, with few (about three) major serrations; lateral margin of pronotum acutely elevated, subserrate; antennal club rather slender, almost symmetrical, ventral margins of segments not noticeably extended; phloeophagous; Australia to New Guinea; 3.1-4.6 mm . . . . *Aricerus*

— Lateral margin of protibia with several socketed teeth, none strongly projecting beyond others (one exception); lateral margins of pronotum rounded; ventral or lateral margin of each antennal club segment weakly to profoundly extended into a sublamellate process except in very primitive species; phloeophagous; North and South America, Europe, N Asia, N Africa, Australia . . . . *Phloeotribus*

***Aricerus* Blandford** [1894b: 133, Type-species: *Aricerus chapuisi* Blandford, subsequent designation by Hopkins 1914: 117. Synonym: *Hylesinosoma* Lea 1910: 143, Type-species: *Hylesinus fici* Lea =*Aricerus eichhoffi* Blandford, monobasic]. Distribution: 3 species from Australia to New Guinea. Monogamous and phloeophagous in *Ficus* limbs.

***Phloeotribus* Latreille** [1796: 50, Type-species: *Hylesinus oleae* Fabricius =*Scolytus scarabaeoides* Bernard, monobasic. Synonyms: *Phloiotribus* Latreille, 1796: 50, inadvertent error in original spelling amended in Latreille 1804: 108, ruled by International Commission on Zoological Nomenclature 1979: 132; *Phloeophthorus* Wollaston 1854: 299, Type-species: *Phloeophthorus perfoliatus* Wollaston, monobasic; *Dryotomus* Chapuis 1869: 46, Type-species: *Dryotomus puberulus* Chapuis, monobasic; *Phthorophloeus* Rey 1883: 128, Type-species: *Phloeophthorus spinulosus* Rey, monobasic; *Elzearius* Guillebeau 1893: 64, Type-species: *Elzearius crenatus* Guillebeau, monobasic; *Eulytocerus* Blandford 1897: 161, Type-species: *Eulytocerus championi* Blandford, monobasic; *Comesiella* Del Guercio 1925: 218, Type-species: *Comesiella sicula* Del Guercio = *Bostrichus brevicollis* kolenati, monobasic; *Neophloeotribus* Eggers 1943: 349, Type-species: *Phloeotribus nubilus* Blandford, designated by Wood 1983: 648; *Dryotomicus* Wood 1962: 76, Type-species: *Dryotomus puberulus* Chapuis, automatic]. Distribution: About 58 species in South America, 27 in North and Central America, 10 in Europe, 4 in N Africa, 1 in Australia. All are monogamous and phloeophagous. Keys: Pfeffer (1972: 31) for Europe, Blandford (1897: 162) for Central America, Wood 1982: 257) for North and Central America.

Tribe Phloeosinini

Phloeosinides Nüsslin [1912b: 273, Type-species: *Phloeosinus* Chapuis, 1869]

DESCRIPTION.—Frons usually dimorphic, male impressed, female flat to convex; eye varying from entire to emarginate to completely divided; antennal funicle 5- to 7-segmented, club flattened, slightly to strongly asymmetrical, with or without sutures; pronotum armed or not; tarsal segment 3 compressed to broad and bilobed; scutellum visible or not; metanotum fused to postnotum.

BIOLOGY.—All are monogamous except for a few species of polygynous *Olonthogaster* and one bigynous *Chramesus*. Most are phloeophagous, although *Dendrosinus* and three species of *Chramesus* are xylophagous and *Hyleops* larvae become xylomycetophagous in the later stages. The parental tunnels are mostly monoramous, with a conspicuous turning niche, a few are rather primitively (unequally) biramous. Eggs are placed in niches and packed in frass. Larval mines tend to follow a definite course away from the parental tunnel and rarely cross one another.

TAXONOMY.—This tribe appears to consist of a diverse assemblage of somewhat distantly related genera or clusters of genera that appear to be relicts from a former much larger group. Their worldwide distribution, diverse structure, and possession of several primitive traits suggest an ancient origin that extends

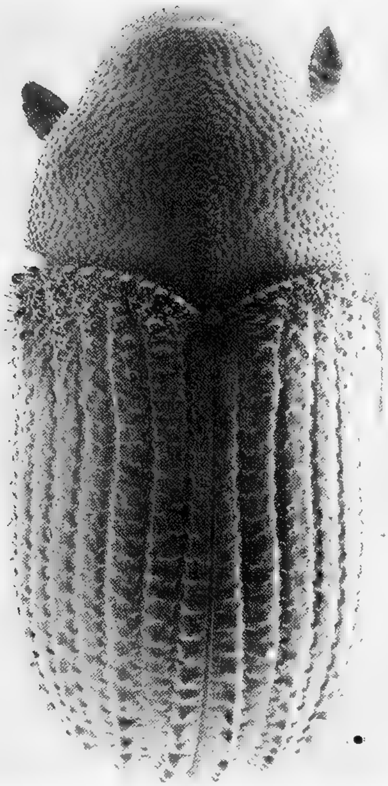


Fig. 40. *Phloeosinus punctatus* LeConte, dorsal aspect of male. (After Bright 1976: 207).

well into the Cretaceous. Within the tribe, two clusters of genera are apparent. *Pseudochramesus* and *Chramesus* (America) are closely related to one another and are the most highly evolved from a structural point of view. *Cladoctonus*, *Phloeosinopsoides*, *Olonthogaster*, and *Phloeosinus* (Fig. 40) form a second cluster of genera to which *Phloeocranus* (Fig. 41) and *Phloeodictica* might form a primitive base. All are Old World genera except that about half of the *Cladoctonus* species occur in tropical America and a segment of *Phloeosinus* has extended into North America in comparatively late Tertiary time. The *Cladoctonus* species of the Philippines (1), Africa (8), and tropical America (6) have apparently changed only slightly since attaining their present generic distribution (perhaps early Tertiary). The American *Dendrosinus* and *Carphotoreus* and the Australian *Hyleops* are not closely related to one another or to the other known generic groups of this tribe.

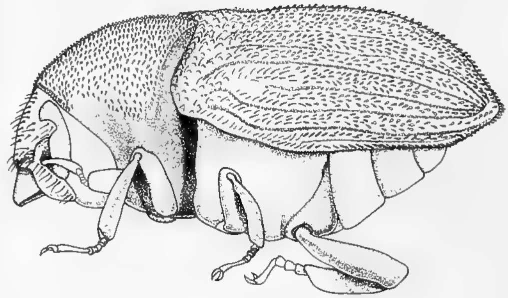


Fig. 41. *Phloeocranus bruchoides* Schedl, lateral aspect of female (tibial denticles omitted).

Key to the Genera of Phloeosinini

1. Interstriae 10 continued to declivity (to level of visible sternum 3); protibia with lateral apical angle produced slightly and armed by three socketed teeth; humeral angles of elytra strongly produced cephalad, largest crenulations at humeral angles; eye deeply emarginate (three-fourths divided); funicle 5-segmented; scutellum not visible; phloeophagous; India to Malaya; 2.5-3.5 mm .... ***Phloeocranus***

— Interstriae 10 not continued behind level of metacoxae; lateral apical angle of protibia not produced (except *Phloeoditica*) 2

2(1). Protibia slender, outer apical angle armed by two closely set, projecting, socketed denticles, one smaller tooth on lateral margin; procoxae rather widely separated by distance equal to width of coxa; funicle 5-segmented, club symmetrical to moderately asymmetrical; pronotum unarmed; scutellum not visible; elytral ground vestiture of circular (rounded) scales; metathoracic wings apparently absent in male of at least one species; phloeophagous; SE Asia; 2.2-2.5 mm .... ***Phloeoditica***

— Protibia more strongly flattened, armed by three or more socketed teeth of equal size; with other combination of characters 3

3(2). Antennal club symmetrical to rather weakly asymmetrical (Fig. 42); eye emarginate, or divided when funicle 5-segmented; procoxae either separated or contiguous; body usually more slender 4

— Antennal club very strongly asymmetrical (Fig. 43), sutures strongly procurved when present; eye entire; funicle 5-segmented; procoxae rather widely separated; body usually very stout; American species 11

4(3). Eye entire; funicle 6- or 7-segmented; pronotum armed or not 5

— Eye weakly emarginate to completely divided; funicle 5-segmented (6-segmented in some *Cladoctonus*); pronotum unarmed by asperities (except weakly armed in *Phloeosinopsoides*) 8

5(4). Funicle 7-segmented; bases of elytra produced anteriorly, each strongly procurved; scutellum visible, elytral notch for its reception very deep, narrow; procoxae very widely separated; pronotum armed or not; body stout, usually black; xylophagous; Mexico to South America; 3.0-5.0 mm . . . . ***Dendrosinus***

— Funicle 6- or 7-segmented; elytral bases not produced; scutellar notch at sutural base of elytra not unusually deep or narrow; procoxae contiguous to moderately separated; smaller . . 6

6(5). Procoxae contiguous; pronotum unarmed; funicle 7-segmented; scutellum obsolete; tarsal segment 3 broad, strongly bilobed; phloeophagous except larvae xylomycetophagous in later stages; Australia; *Araucaria*; 2.4-4.0 mm . . . . ***Hyleops***

— Procoxae separated by about half width of a coxa; funicle 6-segmented; pronotum armed by fine asperities; scutellum visible; tarsal segment 3 narrow; phloeophagous 7

7(6). Body more slender, 2.1 times as long as wide; antennal club almost symmetrical, three sutures indicated, 1 partly septate; posteromesal margin of pronotum almost straight; Mexico; *Alnus*; 2.5-2.7 mm . . . . ***Carphotoreus***

— Body stout, 1.6 times as long as wide; antennal club strongly asymmetrical, suture 1 septate, others not indicated; posteromesal margin of pronotum slightly extended toward scutellum; Congo; 1.8 mm . . . . ***Catenophorus***

8(4). Antennal club subglobular, sutures obsolete or indicated by sparse setae; funicle 5- or 6-segmented; procoxae contiguous; scutellum visible or not; phloeophagous; tropical America, Africa, Philippines; 1.4-2.5 mm . . . . ***Cladoctonus***

— Club flattened, sutures transverse to oblique when present; funicle 5-segmented; procoxae moderately separated; scutellum visible; phloeophagous 8

9(8). Pronotum finely asperate at least in lateral areas; sutures 1 and 2 on antennal club transverse; eye coarsely faceted, anterior margin shallowly, broadly emarginate; elytral ground vestiture almost obsolete, erect setae in rows, flattened, almost scalelike; Taiwan to New Guinea; 1.3-2.5 mm . . . . ***Phloeosinopsoides***

— Pronotum unarmed; sutures 1 and 2 on antennal club oblique; eye more finely faceted, emargination at least one-third as deep as eye width (completely divided in some Asian species); elytral ground vestiture usually more abundant, erect setae slender when ground setae sparse 10

10(9). Eye usually completely divided by an emargination (several exceptions); tarsal segment 3 slender; protibia with two (rarely one to three) apical and subapical socketed teeth, one or two others sometimes on lateral margin; vestiture usually less abundant; male frons usually concave; female frons concave to convex, usually ornamented by a conspicuous brush of hair; color usually reddish brown; SE Asia to New Guinea; mostly in nonconiferous hosts; 1.4-5.5 mm . . . . ***Olonthogaster***

— Eye less than one-half divided by an emargination; tarsal segment 3 broad, emarginate to bilobed; protibia with three or more socketed denticles on apical and subapical margin, four or more smaller teeth on lateral margin; vestiture more abundant; male frons usually shallowly impressed; female frons convex, often with a median carina, vestiture inconspicuous in both sexes; color brown to dark brown; N Africa to N Asia, North America, Australia; mostly in coniferous hosts; 1.4-4.1 mm (*Phloeosinites* Hagedorn presumably fits near here) . . . . ***Phloeosinus***

11(3). Antennal club with sutures strongly procurved, clearly marked by rows of setae and grooves; phloeophagous; S America; 1.3-2.0 mm . . . . ***Pseudochramesus***

— Antennal club without sutures; mostly phloeophagous; North and South America; 1.2-2.7 mm . . . . ***Chramesus***

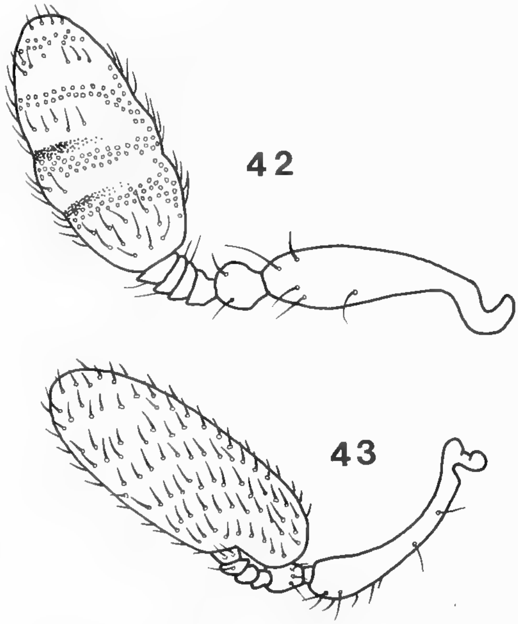


Fig. 42-43. Antennae of Phloeosinini: 42, above *Phloeosinus thujae* (Perris); 43, below, *Chramesus hickoriae* LeConte.

***Phloeocranus* Schedl** [1942: 7, Type-species: *Phloeocranus bruchoides* Schedl, monobasic. Synonym: *Diamerides* Browne 1949: 893, Type-species: *Diamerides litseae* Browne = *Phloeocranus bruchoides* Schedl, original designation]. Distribution: 1 species from India to Indonesia in *Litsea*. This species is monogamous and phloeophagous.

Phloeoditica **Schedl** [1962d: 189, Type-species: *Kissophagus curtus* Eggers, present designation]. Distribution: One species in SE Asia. It breeds in *Pongamia glabra*.

Dendrosinus **Chapuis** [1869: 28, Type-species: *Hyulesinus globosus* Eichhoff, monobasic]. Distribution: 10 species from USA (Florida) and Mexico (Jalisco) to Argentina. All are monogamous and xylophagous. Key: Wood (1982: 283).

Hyleops **Schedl** [1938b: 35, Type-species: *Hyleops glabratus* Schedl, monobasic]. Distribution: 1 species in Australia in *Araucaria* branches. It is monogamous and partly phloeophagous. The later larval stages penetrate the xylem and become xylomycetophagous. Parental tunnels are transversely biramous and without apparent symbiotic fungi.

Carphotoreus **Wood** [1973b: 171, Type-species: *Chaetophloeus alni* Bright, original designation]. Distribution: 1 species in Mexico (Oaxaca). It is monogamous and phloeophagous.

Catenophorus **Nunberg** [1956b: 195, Type-species: *Catenophorus congonus* Nunberg, original designation]. Distribution: 1 species in the Congo. The habits are unknown.

Cladoctonus **Strohmeyer** [1911: 17, Type-species: *Cladoctonus affinis* Strohmeyer, monobasic. Synonyms: *Hoplites* Eggers 1923: 140, Type-species: *Hoplites banosus* Eggers, monobasic, preoccupied; *Hoplitontus* Wood 1961: 2, Type-species: *Hoplites banosus* Eggers, automatic; *Hoplitophthorus* Wood 1961: 2, Type-species: *Hoplitophthorus sentosus* Wood =*Hoplites interruptus* Eggers, original designation]. Distribution: 8 species in Africa, 6 in Cuba to Brazil and Bolivia; 1 in the Philippine Islands. The two species for which habits are known are monogamous and phloeophagous.

Phloeosinopsoides **Schedl** [1964c: 317, Type-species: *Phloeosinopsis triseriatus* Schedl, automatic. Synonym: *Phloeosinopsis* Schedl 1964b: 297, Type-species: *Phloeosinopsis triseriatus* Schedl, original designation, preoccupied]. Distribution: About 8 species from Taiwan to New Guinea. All are monogamous and phloeophagous.

Phloeosinus **Chapuis** [1869: 37, Type-species: *Hylesinus thujae* Perris, subsequent designation by Hopkins 1914: 126]. Distribution: 29 species in North America, about 30 in Asia and adjacent islands, 5 in Europe, 2 in N Africa, and 2 in Australia. All are monogamous and phloeophagous. Most are in coniferous hosts, especially Cupressineae. Keys: Blackman (1942c: 400) and Wood (1982: 287) for North America, Schedl (1950a: 36) for Europe, Murayama (1963: 22) for Japan.

Olonthogaster **Motschulsky** [1866: 401, Type-species: *Olonthogaster nitidicollis* Motschulsky, subsequent designation by Hopkins 1914: 126. Synonyms: *Holonthogaster* Gemminger & Harold 1872: 2676, Type-species: *Olonthogaster nitidicollis* Motschulsky, automatic; *Hyledius* Sampson 1921: 35, Type-species: *Hyledius asper* Sampson, monobasic; *Hylurgulus* Eggers 1927c: 392, Type-species: *Hylurgulus summatranus* Eggers, monobasic; *Phloeosinopsis* Schedl 1936a: 23, Type-species: *Phloeosinopsis armatus* Schedl =*Phloeosinus spinifer* Schedl, original designation]. Distribution: About 25 species from SE Asia to Australia. All are phloeophagous and monogamous except for 2 polygynous species from New Guinea. Hosts include *Lytsea*, *Myristica*, etc.

Phloeosinites **Hagedorn** [1907: 119, Type-species: *Phloeosinites rehi* Hagedorn, subsequent designation by Hopkins 1914: 126]. Distribution: 8 fossil species in Baltic amber (Oligocene). The relationship of this genus to *Phloeosinus* was not determined.

Pseudochramesus **Blackman** [1939: 87, Type-species: *Chramesus acuteclavatus* Hagedorn, original designation]. Distribution: 11 species in South America. The habits have not been reported. Key: Blackman (1939: 88).

Chramesus **LeConte** [1868: 168, Type-species: *Chramesus hicoriae* LeConte, monobasic. Synonyms: *Rhopalopleurus* Chapuis 1869: 46, Type-species: *Rhopalopleurus tuberculatus* Chapuis, subsequent designation by Hopkins 1914: 128; *Thaumasinulus* Reitter 1913: 39, Type-species: *Dendrosinus bonnairei* Reitter =*Chramesus rotundatus* Chapuis, monobasic; *Prochramesus* Wood 1956b: 254, Type-species: *Prochramesus annectans* Wood, original designation]. Distribution: 39 species in South America, 40 in North and Central America and adjacent islands. All are monogamous, except for the bigynous *C. incomptus*, and all are phloeophagous except

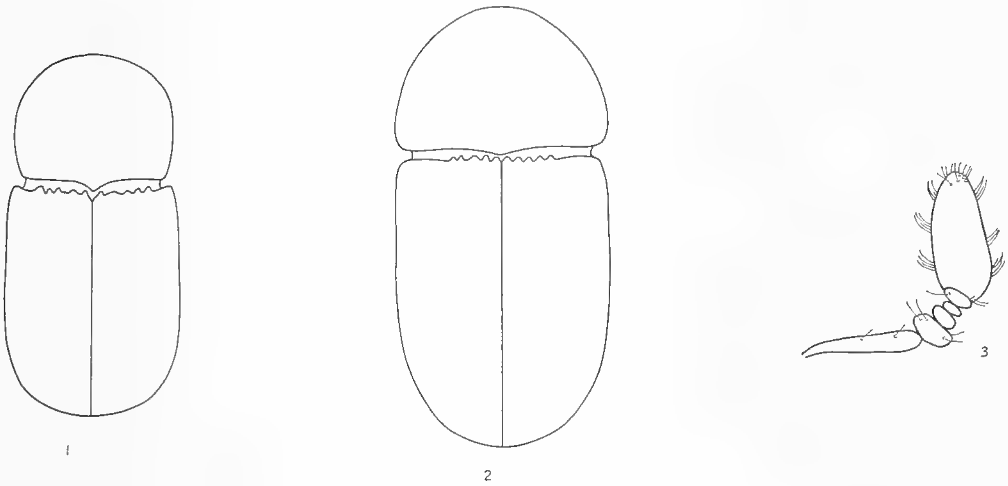


Fig. 44. *Liparthrum* spp.: 1, outline of dorsal aspect of *arizonicum* Wood; 2, outline of dorsal aspect of *albosetum* Bright; 3, outline of antenna of *albosetum*. (After Bright 1968: 639).

for the myelophagous *C. quadridens* and three xylophagous species. Keys: Blackman (1938c: 536), Wood (1982: 316).

Tribe Hypoborini

Hypoborinae Nüsslin [1911: 376, Type-genus: *Hypoborus* Erichson, 1836]

DESCRIPTION.—Frons dimorphic or not, male impressed, female convex or less strongly impressed, except in some *Liparthrum* species this feature is reversed; eye entire; funicle 3- to 6-segmented, club with up to three sutures, sometimes absent; pronotum variously armed in restricted areas; procoxae contiguous; tarsal segment 3 narrow; scutellum not visible; crenulations on elytral bases not continued laterad from interstriae 5; postnotum fused to metatergum (remnants of suture sometimes visible).

BIOLOGY.—All are monogamous and phloeophagous. In all except *Chaetophloeus* the parental gallery is a simple, oval cave. Eggs are packed in frass in niches on the margins of the central cave (*Liparthrum*) or of the egg tunnels (*Chaetophloeus*). Larval mines radiate out from the parental chamber and rarely cross one another; they are visible on the inner surface of peeled bark.

TAXONOMY.—This tribe is sparsely and widely distributed in the warm climates around the world. Except for *Liparthrum* (Fig. 44), which is almost worldwide in the warm areas, the remaining genera are of limited distribution. One is American, 1 Australian, 2 Madagascaran, and 4 African (1 of these reaches nearby areas of Europe and Asia in cultivated fig). It appears to be a relict group that once enjoyed much greater distribution and diversity than at present.

The American genus, *Chaetophloeus*, is quite different structurely and biologically from the remaining closely related genera. Members of this tribe apparently prefer arid or semiarid areas or habitats and tend to be rare. Since they breed in shrubs or small trees of marginal economic importance, it is suspected that a majority of the species await discovery.

Key to the Genera of Hypoborini

1. Funicle 6-segmented, club small, conical, with two straight sutures; Australia; *Acacia*; 1.3 mm . . . . ***Zygophloeus***

— Funicle with 3- to 5-segments; club flattened, sutures present or absent 2

2(1). Protibia strongly flattened, rather broad, lateral apical half armed by a row of 7-10 closely set, socketed teeth; pronotal asperities confined to two or three paired clusters on lateral thirds, each cluster containing 1-5 denticles; funicle 5-segmented, club clearly marked by three sutures; phloeophagous; North and South America; 1.1-2.5 mm . . . . ***Chaetophloeus***

— Protibia slender, lateral margin armed by about four rather widely spaced, socketed teeth; pronotal asperities mostly on median third, more abundant; funicle 3- to 5-segmented 3

3(2). Antennal funicle 5-segmented, club rather broad, sutures very broadly procurved; protibia slender, with one large spine on outer apical angle and four small, socketed denticles on lateral margin; crenulations on basal margins of elytra feeble; body subglabrous; Madagascar; 1.5 mm .... ***Glochiphorus***

— Protibia not armed on outer apical angle by a major spine; antenna variable; elytra bearing setae 4

4(3). Funicle 4- or 5-segmented, club with sutures obscure, club more broadly oval 5

— Funicle 3-segmented, club usually more slender 7

5(4). Antennal funicle 4-segmented (appearing 3-segmented, but 4- or possibly 5-segmented on slide mount), club unmarked by sutures; basal margins of elytra a continuous costa, individual crenulations feebly indicated; anterior half of pronotum asperate; striae not impressed, punctures coarse, deep, wider than interstriae; Madagascar; 1.6 mm .... ***Cryphyophthorus***

— Funicle 4- or 5-segmented; crenulations on basal margins of elytra well-formed; strial punctures smaller; pronotal asperities often present, but less conspicuous 6

6(5). Funicle 4-segmented, club devoid of sutures; meso- and metatibiae slender, about equal to protibia; phloeophagous; S USA to N South America, S Europe and N Africa to China and Micronesia; 0.8-1.5 mm .... ***Liparthrum***

— Funicle 5-segmented, club with three obscure sutures; meso- and metatibiae rather strongly flattened, much wider and more coarsely serrate than protibia; phloeophagous; S Europe, N Africa to Asia Minor; 1.1-1.4 mm ..... ***Hypoborus***

7(4). Antennal club with three distinct sutures; meso- and metathoracic tibiae slender, about equal to protibia; phloeophagous; Africa; 1.2-1.8 mm .. .. ***Styracoptinus***

— Antennal club long and slender, sutures not indicated; scape ornamented by a tuft of long hair; discal interstriae 2 on basal fourth with one tubercle greatly enlarged in male, 3 with four tubercles on posterior half and upper half of declivity; phloeophagous; Africa; 1.6-2.0 mm . ... ***Dacryostactus***

***Zygophloeus* Schedl** [1958b: 215, Type-species: *Zygophloeus australis* Schedl, monobasic]. Distribution: 1 species in *Acacia* in Australia.

***Glochiphorus* Strohmeyer** [1910c: 126, Type-species: *Glochiphorus globosus* Strohmeyer, monobasic]. Distribution: 1 species in Madagascar.

***Chaetophloeus* LeConte** [1876: 382, Type-species: *Hylesinus hystrix* LeConte, monobasic. Synonyms: *Renocis* Casey 1886: 257, Type-species: *Renocis heterodoxus* Casey, monobasic; *Pseudocryphalus* Swaine 1917: 20, Type-species: *Pseudocryphalus brittaini* Swaine =*Renocis heterodoxus* Casey, original designation]. Distribution: 17 species in North America and adjacent islands, 2 in South America. All are monogamous and phloeophagous. Keys: Blackman (1940: 376), Wood (1982: 349).

***Cryphyophthorus* Schedl** [1953c: 294, Type-species: *Cryphyophthorus eggersi* Schedl, original designation]. Distribution: 1 in Sumatra (Indonisia), 1 in Madagascar.

***Liparthrum* Wollaston** [1854: 294, Type-species: *Liparthrum bituberculatum* Wollaston, original designation. Synonyms: *Leiparthrum* Wollaston 1854: 294, invalid error in spelling, amended by Wollaston (1864: 265), International Commission on Zoological Nomenclature (1981: 64) ruled this to be an invalid spelling; *Erineosinus* Blackman 1920: 53, Type-species: *Erineosinus squamosus* Blackman, monobasic; *Phloeochilus* Schedl 1953c: 292, Type-species: *Phloeochilus palaquius* Schedl, original designation; *Phloeotrypetus* Wood 1960a: 16, Type-species: *Phloeotrypetus palauensis* Wood, original designation; *Dacryophthorus* Schedl 1971b: 281, Type-species: *Dacryophthorus brincki* Schedl, original designation]. Distribution: 2 species in South America, 7 in North and Central America; 11 in the Canary and other Atlantic islands, 6 in Europe, 1 in China, 4 in the Indo-Malayan area, and 1 in Micronesia. All are monogamous and phloeophagous. Keys: Schedl (1959a: 36) for the genus, Wood (1982: 364) for North and Central America.

***Hypoborus* Erichson** [1836: 62, Type-species: *Hypoborus fici* Erichson, monobasic]. Distribution: 1 species from S Europe, N Africa, and SW Asia in cultivated fig. Monogamous and phloeophagous.

***Styracoptinus* Wood** [1962: 77, Type-species: *Styracopterus murex* Blandford, automatic. Synonyms: *Styracopterus* Blandford 1896c: 323, Type-species: *Styracopterus murex* Blandford, monobasic, preoccupied; *Afrotrypetus* Bright 1981b: 113, Type-species: *Afrotrypetus euphorbiae* Bright, original designation]. Distribution: About 5 species in

S Africa. All are apparently monogamous and phloeophagous.

Dacryostactus **Schaufuss** [1905: 79 (reprint p. 3), Type-species: *Dacryostactus kolbei* Schaufuss, monobasic]. Distribution: 1 species in Africa. Monogamous and phloeophagous.

Tribe Polygraphini

Polygraphidae Chapuis [1869: 48, Type-genus: *Polygraphus* Erichson, 1836]
Carphoboridae Nüsslin [1911: 376, Type-genus: *Carphoborus* Eichhoff, 1864]

DESCRIPTION.—Frons dimorphic, male variously impressed and sparsely pubescent, female concave to convex and usually ornamented by conspicuous setae; eye emarginate to completely divided; antennal funicle 5- or 6-segmented, club slightly to strongly flattened, symmetrical to strongly asymmetrical, with or without sutures; procoxae contiguous; tarsal segment 3 slender; pronotum unarmed; scutellum not visible; crenulations on bases of elytra either individual (separate) or represented by a continuous costa (*Serrastus*), continued to humeral angle; metanotum fused to its postnotum.

BIOLOGY.—All are phloeophagous. *Carphobius* and some *Polygraphus* are monogamous; apparently *Chortastus* and *Serrastus* share this habit; *Carphoborus* (Fig. 45) and most *Polygraphus* are polygynous. Parental tunnels are monoramous or biramous in monogamous forms and radiate in polygynous forms. The nuptial chamber is unusually large in most species. Eggs are packed in frass in niches. Larval mines wander considerably and have a greater tendency to cross one another than in most other tribes.

TAXONOMY.—In my initial study of the tribes of Scolytidae (Wood 1978), the Polygraphini were reluctantly given tribal status only after much hesitation and the pondering of many questions. Since then, all reservations have been dismissed. Although quite specialized in several respects, representatives of two genera (*Serrastus*, *Polygraphus*) have the outer apical angle of the protibia produced beyond the tarsal insertion and are armed as in primitive representatives of other unspecialized tribes. The tribe generally appears to have been derived from the same ancestral stock as the Phloeosinini, but

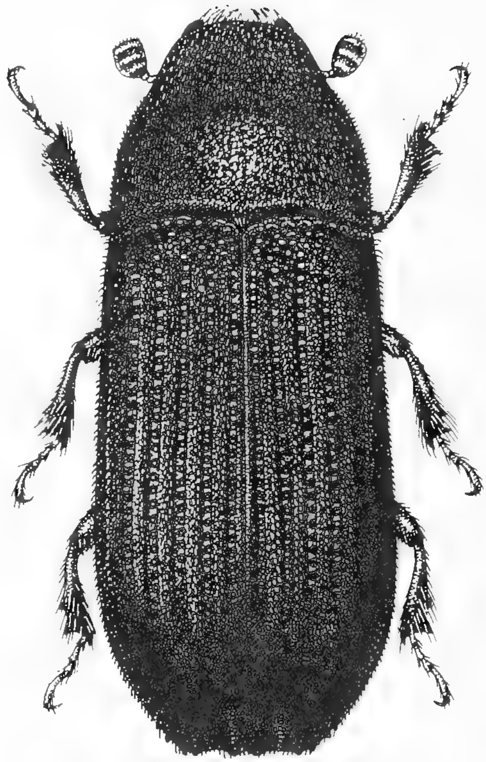


Fig. 45. *Carphoborus pinicolens* Wood, dorsal aspect of female. (After Bright and Stark 1973: 155).

the one known species of *Phloeographus* bears a remarkable superficial resemblance to certain *Tomicus* species (Hylesinini).

The genera form a rather compact unit without conspicuous divisions. Four small genera are exclusively African (*Serrastus*, *Chortastus*, *Phloeographus*, *Cardroctonus*), one is Malayan (*Bothinodroctonus*), and one is American (*Carphobius*). The larger genus *Carphoborus* is primarily North American and probably originated there from stock derived from Asia. European and Asian species of *Carphoborus* appear to have been derived from the more primitive and diverse American fauna. The largest genus, *Polygraphus*, is largely African, with strong representation in Europe and Asia, and with three species in northern North America. The absence of this group in South America suggests either an origin since early Tertiary, if Africa were the site, or else an origin in tropical Eurasia. *Polygraphus* reached North America in comparatively recent time, *Carphoborus* and *Carphobius* much earlier. Eurasian *Car-*

phoborus were probably derived from a secondary radiation that moved from North America to Asia. *Carphobius* apparently represents a relict from a very early ancestral stock not now represented elsewhere.

Key to the Genera of Polygraphini

1. Basal margins of elytra armed by a continuous costa; protibia very slender, its median apical mucro bent laterad, about one lateral denticle present, posterior face asperate; funicle 5-segmented; club strongly flattened, moderately asymmetrical, sutures not indicated; phloeophagous; Africa; 1.8-2.0 mm .... ***Serrastus***

— Basal margins of elytra serrate, armed by a row of crenulations; protibia more broadly flattened, lateral margin armed by several socketed denticles 2

2(1). Funicle 5-segmented (5- or 6-segmented in *Polygraphus*, if 6-segmented then eye completely divided); male frons armed by a median pair of tubercles near upper level of eyes; vestiture of abundant scales (except glabrous in some *Bothinodroctonus*) 3

— Funicle 6-segmented; eye never divided into two parts; male frons unarmed by median tubercles; vestiture hairlike or sparse if scalelike 7

3(2). Eye completely divided by a deep emargination (some Asian and African species only emarginate); antennal club rather strongly flattened, asymmetrical, devoid of sutures; phloeophagous; North America, Asia, Europe, Africa; 1.5-5.5 mm .... ***Polygraphus***

— Eye less than half divided by an emargination; antennal club symmetrical (or nearly so), clearly marked by sutures 4

4(3). Sutures of antennal club procurved; vestiture sparse, in uniseriate rows on interstriae; tropical Africa 5

— Sutures of antennal club straight or nearly so; vestiture much more abundant; northern hemisphere 6

5(4). Antennal club with three weakly procurved sutures indicated, apex strongly acuminate; vestiture sparse, of uniseriate rows on declivity; declivital interstriae 2 slightly impressed, unarmed, 1 and 3 armed by small tubercles; SW Africa; 2.2 mm .... ***Phloeographus***

— Antennal club with suture 1 partly septate, 1 weakly, 2 moderately procurved; strial punctures very fine; Africa; 1.3-2.0 mm . ***Cardroctonus***

6(4). Male frons shallowly impressed below upper level of eyes, female usually convex; vestiture of abundant scales; antennal club moderately large, flattened; phloeophagous; North America, N Asia, Europe, N Africa; 1.4-2.6 mm .... ***Carphoborus***

— Male frons profoundly excavated from eye to eye from epistoma to well above eyes, female similarly but less strongly excavated; antennal club small, more nearly conical; vestiture confined to a few interstrial setae on and near declivity; phloeophagous; India to Malaya; 1.8-2.5 mm .. .. ***Bothinodroctonus***

7(3). Antennal club symmetrical, with three transverse sutures indicated; vestiture abundant, hairlike; phloeophagous; North America; 1.6-2.1 mm .... ***Carphobius***

— Antennal club rather strongly asymmetrical, part of suture 1 indicated, strongly oblique; vestiture usually confined to declivity, scalelike; phloeophagous; Africa; 2.5-5.3 mm ... ***Chortastus***

Serrastus **Nunberg** [1969: 392, Type-species: *Serrastus ivoriensis* Nunberg =*Chortastus similis* Eggers, monobasic]. Distribution: 2 species in Africa (Ghana to Zaire). They are monogamous and phloeophagous.

Phloeographus **Wood** [1984: 229, Type-species: *Phloeographus mamibiae* Wood, original designation]. Distribution: 1 species in Africa (apparently Namib Desert, SW Africa).

Cardroctonus **Schedl** [l966b: 361, Type-species: *Cardroctonus orientalis* Schedl, original designation]. Distribution: 2 species in Africa.

Polygraphus **Erichson** [1836: 57, Type-species: *Hylesinus pubescens* Fabricius =*Dermestes poligraphus* Linnaeus, monobasic. Synonyms: *Lepisomus* Kirby 1837: 193, Type-species: *Apate* (*Lepisomus*) *rufipennis* Kirby, subsequent designation by Hopkins 1914: 124; *Spongotarsus* Hagedorn 1908: 372, Type-species: *Spongotarsus quadrioculatus* Hagedorn, monobasic; *Pseudopolygraphus* Seitner 1911: 105, Type-species: *Polygraphus grandiclava* Thomson, subsequent designation by Hopkins 1914: 128; *Ozophagus* Eggers 1919: 234, Type-species: *Ozophagus camerunus* Eggers, subsequent designation by Wood 1982: 386; *Urdugraphus* Beeson 1941: 301, nomen nudum]. Distribution: 3 species in North America, about 45 in Asia and adjacent islands, 6 in Europe, about 45 in Africa and Madagascar. Most are polygynous, although monogamy occurs in some Asian and African species. All are phloeophagous. Keys: Schedl (1955a: 5) for Europe and part of Asia, Murayama (1956: 278) for Japan, Wood (1982: 387) for North America.

Carphoborus **Eichhoff** [1864: 27, Type-species: *Hylesinus minimus* Fabricius, monobasic. Synonym: *Estenoborus* Reitter 1913: 58, Type-species: *Hylesinus perrisi* Chapuis,

monobasic]. Distribution: 21 species in North America, 14 in Europe and Asia, 2 in N Africa. All are polygynous and phloeophagous. Keys: Pfeffer (1914: 169) for Europe, Balachowsky (1949: 143) for France, Wood (1954a: 507, 1982: 372) for North America.

***Bothinodroctonus* Schedl** [1969: 208, Type-species: *Bothinodroctonus bicinctus* Schedl, monobasic]. Distribution: 4 species from India to Borneo and China. One species is phloeophagous in *Odina*.

***Carphobius* Blackman** [1943c: 398, Type-species: *Carphobius arizonicus* Blackman, original designation]. Distribution: 3 species in North America (Arizona to Guatemala). All are monogamous and phloeophagous in conifers. Key: Wood (1982: 369).

***Chortastus* Schaufuss** [1905: 15 (reprint p. 8), Type-species: *Chortastus camerunus* Schaufuss, monobasic. Synonym: *Afrochramesus* Schedl 1971a: 197, Type-species: *Afrochramesus baguenai* Schedl, original designation]. Distribution: 7 species in Africa. Apparently all are monogamous and phloeophagous.

Subfamily Scolytinae

Scolytarii Latreille [1807: 273, Type-genus: *Scolytus* Geoffroy, 1762]

In previous classifications, this subfamily has been divided into two or more major divisions equivalent to subfamilies. However, it appears that this unit contains both the most primitive elements of the family that are most closely related to primitive Platypodidae and also the main evolutionary thrust of the platypodid-scolytid group. This diversity makes characterization of the subfamily rather difficult.

Members of this subfamily have the bases of the elytra simple, forming a straight, transverse line across the body. A large, flat scutellum is usually visible. The elytral bases are weakly subcostate in some Scolytini, Ctenophorini, and Cryphalini. The body tends to be more elongate, with specialization directed toward cylindrical compaction and the xylomycetophagous habit. A broadly oval body outline is usually confined to primitive, phloeophagous genera. Armed elytral bases that suggest a relationship to the Hylesininae occur in Ctenophorini (*Cnemonyx*, allies of *galeritus*).

Five clusters of relationship are recognized within the subfamily. Progressing from primitive to the more specialized, these include: (1) Ctenophorini, Scolytini, and Scolytoplatypodini; (2) Micracini and Cactopinini; (3) Carphodicticini, Ipini, Dryocoetini, Crypturgini, Xyloterini, and Xyleborini; (4) Xyloctonini and Cryphalini, and (5) Corthylini. Of these, the Corthylini are by far the most distinctive from an anatomical point of view.

Tribe Scolytini

Scolytarii Latreille [1807: 273, Type-genus: *Scolytus* Geoffroy, 1762]

Camptoceridae Chapuis [1869: 49, Type-genus: *Camptocerus* Latreille, 1829]

DESCRIPTION.—Frons usually strongly dimorphic, male variously impressed, female flat to convex, one or both often ornamented by hair; posterior face of head truncate; eye oval, entire; scape short to elongate, funicle 7-segmented, club rather large, flattened, sutures present or not; pronotum unarmed, its lateral margins costate; protibia (usually all three tibiae) unarmed on lateral margin, outer apical angle extended into a spine curving toward and exceeding inner apical angle, socketed denticles never present; metapleural suture descending subvertically to groove receiving groove on costal margin of elytra then turning abruptly and continuing parallel to groove to near metacoxal process; in two genera venter of abdomen ascends conspicuously to meet apex of weakly declivous elytra.

BIOLOGY.—All are monogamous except for a few neotropical and one European bigynous *Scolytus*. *Camptocerus* species are xylomycetophagous; those in the other three genera are phloeophagous. Parental galleries are biramous, except for a few that are monoramous. In *Camptocerus*, a biramous, transverse tunnel without niches is usually made in the cambium region, then a radial egg tunnel (sometimes branched) is extended from it into the xylem. Eggs are deposited in niches in this radial tunnel. The larval mines of phloeophagous species follow a definite course and rarely cross one another. *Camptocerus* larvae enlarge the egg niche into a cradle just large enough to accommodate the mature beetle, somewhat similar to some other ambrosia beetles.

TAXONOMY.—Except for the Eurasian element of *Scolytus*, members of this tribe are exclusively American. Their obvious origin is neotropical. Some members of this group resemble the primitive ancestral line that probably gave rise to the Hylesininae; in fact, some *Cnemonyx* have crenulations on the basal margins of the elytra. They also appear closely allied to the stock from which Platypodidae diverged. The four genera assigned here form a compact group, although the *Cnemonyx* appear more primitive and, in some respects, overlap the other three.

Scolytus appears to have reached North America from South America by the beginning of the Tertiary, when a secondary radiation occurred. Elements of this radiation then reached Eurasia, where another radiation occurred that was based on a progressively reduced gene pool. The number of Eurasian species in this genus now may equal or exceed the American component, although the anatomical and biological diversity there is greatly reduced.

Key to the Genera of Scolytini

1. Scutellar area of interstriae 1 not depressed, scutellum flush (even) with elytral bases; basal margins of elytra with a fine raised line (some *Cnemonyx* with crenulations instead), outline of anterior margins form a continuous, straight, transverse line with scutellum; ventral profile of abdomen ascending gradually 2

— Scutellum depressed, subtriangular, apically (posteriorly) pointed; elytral bases depressed in scutellar area, appearing emarginate in median area; ventral profile of abdomen usually ascending abruptly at segment 2 3

2(1). Antennal club usually with two or three sutures clearly marked by setae; scutellum small, longer than wide, often convex; apical margin of meso- and metathoracic tibiae commonly bearing tubercles on anterior edge in addition to inner and outer apical spines; usually more coarsely sculptured; phloeophagous; USA and Mexico to Argentina; 1.0-3.9 mm .... ***Cnemonyx***

— Antennal club with suture 1 (only) marked internally by a partial septum; scutellum flat, 1.5 or more times as wide as long; meso- and metathoracic tibiae acutely margined on apical anterior edge, without supplemental denticles; usually very finely sculptured; xylomycetophagous; Central and South America; 2.6-8.5 mm .... ***Camptocerus***

3(1). Basal portion of costal margin of elytra deeply, broadly excised, metepisternum conspicuously expanded into this notch (Fig. 46); abdomen abruptly flexed upward at posterior margin of segment 2; phloeophagous, tropical; Mexico (Oaxaca) and Cuba to Argentina; 1.6-3.5 mm .. .. ***Scolytopsis***

— Costal margin of elytra normal (straight) and overlapping metepisternum; abdomen flexed upward from anterior margin of segment 2; phloeophagous; North and South America, Europe, N Asia, N Africa; 1.3-5.5 mm ..... ***Scolytus***

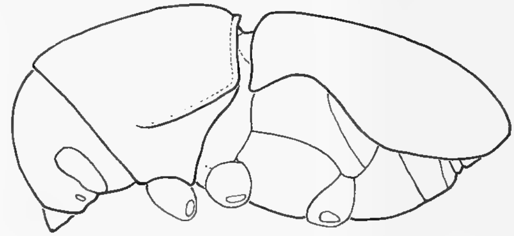


Fig. 46. *Scolytopsis puncticollis*, female. Note emarginate costal margin of elytron.

Cnemonyx **Eichhoff** [1868a: 150, Type-species: *Cnemonyx galeritus* Eichhoff, monobasic. Synonyms: *Ceratolepis* Chapuis 1869: 52, Type-species: *Ceratolepis jucundus* Chapuis, monobasic; *Loganius* Chapuis 1869: 52, Type-species: *Loganius flavicornis* Chapuis, monobasic; *Minulus* Eggers 1912b: 206, Type-species: *Minulus barbatus* Eggers, monobasic; *Coptodryas* Schedl 1948b: 262, Type-species: *Coptodryas hylurgoides* Schedl. monobasic; *Coptosomus* Schedl 1952a: 363, Type-species: *Coptodryas hylurgoides* Schedl, automatic]. Distribution: 19 species in USA (Florida), Mexico, and Central America, about 27 in South America and adjacent islands. All are monogamous and phloeophagous. Keys: Blandford (1896d: 128) for Central America, Wood (1982: 394) for North and Central America.

Camptocerus **Latreille** [1829: 91, Type-species: *Hylesinus aeneipennis* Fabricius, monobasic]. Distribution: 19 species from Central and South America. All are monogamous and xylomycetophagous. Key: Wood 1982: 412 for Central America.

Scolytopsis **Blandford** [1896d: 120, 123, Type-species: *Scolytopsis puncticollis* Blandford, monobasic]. Distribution: 7 species from Cuba and Mexico (Oaxaca) to Argentina. All are phloeophagous and monogamous. Key: Wood (1982: 417) for Central America.

Scolytus **Geoffroy** [1762: 309, Type-species: *Bostrichus scolytus* Fabricius, desig-

nated by the International Commission on Zoological Nomenclature (China 1962: 3). Synonyms: *Ekkoptogaster* Herbst 1793: 124, Types-species: *Bostrichus scolytus* Fabricius, designated by Hopkins 1914: 121; *Coptogaster* Illiger 1807: 321, Type-species: *Bostrichus scolytus* Fabricius, designated by Hopkins 1914: 118; *Eccoptogaster* Gyllenhal 1813: 346, an isotypical emendation of *Ekkoptogaster* Herbst; *Scolytochelus* Reitter 1913: 23, Type-species: *Ips multistriatus* Marsham, designated by Wood 1982: 419; *Ruguloscolytus* Butovitsch 1929: 20, Type-species: *Bostrichus rugulosus* Müller, designated by Wood 1982: 419; *Archaeoscolytus* Butovitsch 1929: 21, 23, Type-species: *Scolytus claviger* Blandford, monobasic, not a genus-group name, no status; *Spinuloscolytus* Butovitsch 1929: 21, 24, Type-species: *Ips multistriatus* Marsham, present designation, not a genus-group name, no status; *Tubuloscolytus* Butovitsch 1929: 21, 33, Type-species: *Eccoptogaster intricatus* Ratzeburg, present designation, not a genus-group name, no status; *Pygmaeoscolytus* Butovitsch 1929: 21, 28, Type-species: *Bostrichus pygmaeus* Fabricius, present designation, not a genus-group name, no status; *Pinetoscolytus* Butovitsch 1929: 22, 48, Type-species: *Scolytus marawitzi* Semenov, monobasic, not a genus-group name, no status; *Confusoscolytus* Tsai, Yin, & Huang 1962: 4, 14, Type-species: *Eccoptogaster confusus* Eggers, monobasic]. Distribution 28 species in North and Central America, about 29 in South America, 47 in Asia, Europe, and N Africa. Monogamous, except for 1 European and about 20 Central and South American bigynous species, and all are phloeophagous. Keys: Blackman (1934: 6) for North America, Schedl (1937a: 156) for South America and (1948a: 4) for Europe, Michalski (1973: 137) for Europe and Asia, Wood (1982: 420) for North and Central America.

Tribe Ctenophorini

Ctenophoridae Chapuis [1869: 49, Type-genus: *Ctenophorus* Chapuis, 1869 = *Scolytodes* Ferrari, 1867]

Problechilidae Eichhoff [1878a: 34, 46, 167, 298, Type-genus: *Problechilus* Eichhoff, 1878 = *Gymnochilus* Eichhoff, 1867]

Hexacolidae Eichhoff [1878a: 35, 57, 306, Type-genus: *Hexacolus* Eichhoff, 1868 = *Scolytodes* Ferrari, 1867]

DESCRIPTION.—Frons usually dimorphic, male impressed and female flat to convex in *Pycnarthrum* and *Gymnochilus*, sexual differences obscure in *Microborus*, male convex and female variously sculptured and ornamented in *Scolytodes*; posterior face of head truncate; eye usually elongate, entire to sinuate; scape elongate, funicle 6- or 7-segmented, club with or without sutures; pronotum armed or not, its lateral margins costate; procoxae widely separated; protibia with one or more socketed denticles on lateral margin, spine on lateral apical angle usually extending beyond level of tarsal insertion; pleural suture about as in Scolytini.

BIOLOGY.—All are monogamous, except for a few polygynous *Scolytodes*. All are phloeophagous, except for the xylophagous *Scolytodes multistriatus* Wood and species that infest *Cecropia* leaf petioles. Parental galleries vary from a simple to an elongate cave to stellate in *Scolytodes*; they are biramous in *Pycnarthrum* and *Gymnochilus* and indefinite, nondirectional, and without definite pattern in *Microborus*. The eggs may be scattered loosely in the parental chamber or placed in crude niches in *Scolytodes*; definite niches are formed in *Pycnarthrum* and *Gymnochilus*; they were not observed in *Microborus*. The larvae usually feed communally in *Scolytodes*; they form individual mines that follow a somewhat definite direction in *Pycnarthrum* and *Gymnochilus*; they are individual and without a definite direction in *Microborus*. Symbiotic relationships with fungi were not observed.

TAXONOMY.—The tribe is restricted to the American tropics, except that *Microborus boops* Blandford was introduced into tropical Africa. *Scolytodes* and *Microborus* are closely related to one another. *Pycnarthrum* and *Gymnochilus* are remotely related to those genera and to one another. *Pycnarthrum* could easily be placed in Hylesinini. This tribe occupies a position intermediate between the Scolytini and the more highly evolved tribes in this subfamily. In all members the outer apical angle of the protibia projects beyond the tarsal insertion, a primitive feature shared by primitive members of several other tribes. It is the Ctenophorini protibia, not the type found in Scolytini, that appears to resemble the ancestral type of all

scolytids. The eye shape, usually unarmed pronotum, presence of interstriae 10, simple sculpture of the elytra, the elytral locking mechanism, and diversity of habits all suggest that, when considered as a whole unit, this is probably the most primitive of all of the tribes of Scolytidae. It is clearly of neotropical origin and has spread into southern North America only recently. This phyletic line is represented in the Old World by Scolytoplatypodini, a group that has diverged significantly in both structure and habits.

Key to the Genera of Ctenophorini

1. Eyes elongate, approximate above and below, coarsely faceted, shallowly emarginate; entire surface of pronotum smooth and punctured, not armed 2
— Eye oval, enitre, finely faceted; pronotum asperate anteriorly or, if smooth, then anterior margin of elytra bearing a fine, raised line 3
2(1). Antennal club subglobular, about as long as wide, sutures not clearly indicated; pronotum longer than wide, its lateral margins straight or feebly constricted; vestiture hairlike, usually sparse; small, slender species; phloeophagous; Central and N South America, Jamaica, Africa; 1.1-1.5 mm . . . . . ***Microborus***
— Antennal club asymmetrically flattened, pointed, at least 1.5 times as long as wide, sutures 1 and 2 clearly marked by setae; pronotum wider than long, its lateral margins arcuate; vestiture of abundant, short, bristlelike scales; larger, stouter species; phloeophagous; Florida and Texas to Brazil; 1.3-2.1 mm . . . . ***Pycnarthrum***
3(1). Antennal funicle 7-segmented, club large, broad, usually with procurved sutures or sutures obsolete; elytral vestiture consisting of abundant, minute hair and sparse interstrial rows of long, erect, scalelike bristles; summit of pronotum on basal third, asperities on anterior area coarse; elytral base without a fine, raised line; phloeophagous; Mexico (Puebla) to Brazil and Bolivia; 1.5-2.3 mm . . . . . ***Gymnochilus***
— Antennal funicle 6-sègmented, club small, sutures present or not; elytral vestiture sparse (usually), hairlike; pronotal asperities fine, if present; summit at middle or indefinite; basal margins of elytra marked by a fine, raised line; mostly phloeophagous; Florida and Mexico to Argentina; 0.9-3.5 mm . . . . . ***Scolytodes***

***Microborus* Blandford** [1897: 175, Type-species: *Microborus boops* Blandford, monobasic. Synonym: *Pseudocrypturgus* Eggers 1919: 236, Type-species: *Pseudocrypturgus camerunus* Eggers =*Microborus boops* Blandford, monobasic]. Distribution: 8 species from Jamaica and Mexico to South America, 1 (*boops*) was introduced into tropical Africa. All are monogamous and phloeophagous. Key: Wood (1982: 452) for Central America.

***Pycnarthrum* Eichhoff** [1878a: 41, 104, Type-species: *Pycnarthrum gracile* Eichhoff =*Hypoborus* (?) *hispidus* Ferrari, subsequent designation by Hopkins 1914: 128. Synonyms: *Nemobius* Chapuis 1869: 41, Type-species: *Nemobius lambottei* Chapuis =*Hypoborus* (?) *hispidus* Ferrari, subsequent designation by Hopkins 1914: 128, preoccupied; *Monebius* Hopkins 1914: 125, Type-species: *Nemobius lambottei* Chapuis =*Hypoborus* (?) *hispidus* Ferrari, automatic; *Nomebius* Navas 1915: 34, Type-species: *Nemobius lambottei* Chapuis =*Hypoborus* (?) *hispidus* Ferrari, automatic]. Distribution: About 15 species in USA (S Florida) and Mexico to Brazil. All are monogamous and phloeophagous. Key: Wood (1982: 455) for North and Central America.

***Gymnochilus* Eichhoff** [1868b: 399, Type-species: *Gymnochilus zonatus* Eichhoff, monobasic. Synonyms: *Problechilus* Eichhoff 1878a: 46, 167, Type-species: *Gymnochilus zonatus* Eichhoff, automatic; *Meringopalpus* Hagedorn 1905: 547, Type-species: *Meringopalpus fallax* Hagedorn =*Gymnochilus zonatus* Eichhoff, monobasic]. Distribution: About 14 species in Mexico to Brazil and Bolivia. All are monogamous and phloeophagous. Key: Wood 1982: 462) for North and Central America.

***Scolytodes* Ferrari** [1867: 77, Type-species: *Scolytodes laevigatus* Ferrari, monobasic. Synonyms: *Hexacolus* Eichhoff 1868b: 399, Type-species: *Hexacolus glaber* Eichhoff, monobasic; *Ctenophorus* Chapuis 1869: 49, Type-species: *Ctenophorus laevigatus* Chapuis =*Hexacolus levis* Blackman, monobasic; *Prionosceles* Blandford 1897: 177, Type-species: *Prionosceles atratus* Blandford, subsequent designation by Hopkins 1914: 128; *Epomadius* Blandford 1897: 179, Type-species: *Epomadius culcitatus* Blandford, monobasic; *Erineophilus* Hopkins 1902: 34, Type-species: *Erineophilus schwarzi* Hopkins, original designation; *Hylocurosoma* Eggers 1940: 138, Type-species: *Hylocurosoma striatum* Eggers, monobasic; *Hexacolinus* Schedl 1963a: 217, Type-species: *Hexacolinus minutissimus* Schedl =*Scolytodes minutissimus* Schedl, original designation; *Cryphalo-*

philus Schedl 1970b: 358, Type-species: *Cryphalophilus afer* Schedl, monobasic]. Distribution: 57 species in USA (S Florida) to Panama, about 60 in South America. Both monogamy and polygyny are common in the genus; habits are diverse, but include phloeophagy, myelophagy, and one is xylophagous. Eggs are usually placed in clusters in galleries; crude egg niches occur in some species, particularly those that make stellate parental tunnels. Key: Wood 1982: 467) for North and Central America.

Tribe Scolytopltypodini

Scolytoplatypini Blandford [1893: 425, Type-species: *Scolytoplatypus* Schaufuss, 1890]

Taeniocerini Blandford [1893: 428, Type-genus: *Taeniocerus* Blandford, 1893 =*Scolytoplatypus* Schaufuss, 1890]

Spongocerinae Hagedorn [1909: 162, Type-genus: *Spongocerus* Blandford, 1893 =*Scolytoplatypus* Schaufuss, 1890]

DESCRIPTION.—Frons dimorphic, male concave, female convex; posterior face of head truncate; eye oval, entire; scape elongate, funicle 6-segmented, club flattened, without sutures; pronotum unarmed, usually constricted on posterior half, female with median mycetangium; procoxae widely separated; protibia with outer apical process prominent, recurved, outer margin without socketed denticles; scutellum not visible, except small in one species; basal margins of elytra usually slightly elevated along a continuous costate line.

BIOLOGY.—All are monogamous and xylomycetophagous. Eggs are deposited in niches. Larvae are reared in individual cradles somewhat similar to those of other ambrosia beetles.

TAXONOMY.—The unique genus *Scolytoplatypus* appears to be a highly specialized geographical replacement of the neotropical *Scolytodes*. It appears to be the only Old World representative derived from the same ancestral stock as the Ctenophorini. A careful study of *Scolytoplatypus* shows quite clearly how the transition from unsocketed tibial spines to socketed tibial teeth (derived from setae) took place (Wood 1978). This transition occurred well after Platypodidae had diverged from the main ancestral line and after family characters for Scolytidae had been fixed.

Scolytoplatypus **Schaufuss** [1890: 31, Type-species: *Scolytoplatypus permirus* Schaufuss, monobasic. Synonyms: *Spongocerus* Blandford 1893: 431, Type-species: *Scolytoplatypus tycon* Blandford, subsequent designation by Hopkins 1914: 129; *Taeniocerus* Blandford 1893: 431, 437, Type-species: *Scolytoplatypus mikado* Blandford, subsequent designation by Hopkins 1914: 130; *Strophionocerus* Sampson 1921: 36, Type-species: *Scolytoplatypus mikado* Blandford, automatic]. Distribution: 9 species in Africa, 3 in Madagascar, 17 from Asia to Indonesia, New Guinea, and the Philippines. All are monogamous and xylomycetophagous. Keys: Browne (1971: 113) for Africa, Schedl (1975: 219) for the genus.

Tribe Micracini

Micracides LeConte [1876: 346, 367, Type-genus: *Micracis* LeConte, 1868]

Hylocuridae Eichhoff [1878a: 298, 306, Type-genus: *Hylocurus* Eichhoff, 1872]

DESCRIPTION.—Frons usually dimorphic; either sex may be variously impressed, sculptured, or ornamented by setae, female frons often concave, male frons rarely concave (two species); dorsomedian occipital area usually extended slightly caudad; eye oval to elongate, entire to sinuate; scape very short to elongate, strongly flattened to slender, ornamented or not; funicle 6-segmented (5-segmented in *Miocryphalus*, Africa), club with or without sutures; pronotum asperate on anterior half, lateral margins rounded; protibia usually with sides parallel, socketed denticles usually confined to apical margin; procoxae usually distinctly separated (contiguous in three African genera); subplumose setae almost always present.

BIOLOGY.—All American genera are bigynous, except that *Micracisella* is monogamous; habits of African genera are largely unreported. Most species occur in broadleaf trees and shrubs in desert or semidesert areas. *Stenoclyptus*, *Phloeocleptus*, and most *Pseudothysanoes* are phloeophagous; *Thysanoes*, *Micracis*, and *Hylocurus* are xylophagous; the species of *Micracisella* are myelophagous in small twigs. Details of their life cycle are poorly known, except that the development of most species is very slow.

TAXONOMY.—The tribe occurs in North and South America and Africa, with one species in

TABLE 2. A comparison of American and African genera of Micracini arranged in order of structural complexity, with the first member in each cluster forming geographical replacements of one another on the same horizontal line. Other genera in each cluster from the same continent are thought to have been derived from the first member of that cluster.

American genera	African genera
Pseudothysanoes	*Lanurgus*
Stenoclyptus	*Traglostus*
Thysanoes	*Saurotocis*
—	*Miocryphalus*
Phloeocleptus	*Phloeocurus*
Hylocurus	
Micracis	*Pseudomicracis*
Micracisella	

N Asia (China). Almost every American genus has a closely allied counterpart in Africa; obviously the generic traits were rather well established before the faunas were separated prior to early Tertiary, but some modification continued after isolation. The Asiatic *Pseudothysanoes mongolica* (Sokanovskii) was obviously derived from American stock much more recently. Because most of the species in this group breed in small twigs and branches of trees and shrubs having little or no economic importance, they are regarded by forest biologists as scientific curiosities and, consequently, are poorly known.

As seen in Table 2, three clusters of genera in this tribe are represented in both America and Africa. The first species in each cluster is a geographical replacement of its counterpart on the other continent, and it is considered to have given rise to the other genera within its own cluster on its own continent. *Miocryphalus* is unrepresented in America and is thought to have been derived very early from a specialized representative of the ancestral stock. The allies of this genus or its ancestor could possibly have given rise to ancestral Xyloctonini and Cryphalini.

Whereas primitive Micracini appear to be allied to the ancestral stock that produced Carphodicticini, I see no clue as to where these groups connect to more primitive Scolytinae, except that it apparently was near the Ctenophorini. The Micracini appear to be the only possible ancestral group for the Cactopinini; however, the connection is remote and obscure at best.

Key to the Genera of Micracini

1. Elytra broadly rounded behind (except subacuminate in *Pseudothysanoes mucronatus*); protibia usually much more slender, less strongly flattened (except *Thysanoes*); lateral margins of antennal club constricted at sutures 1 and (usually) 2, except when sutures absent (American species) or sutures procurved (African species) 2

— Elytral apices acuminate (partly lost in some *Micracisella*), usually mucronate; protibia more strongly flattened, at least apically (exceptions in African species); antennal club without constrictions at sutures, sutures always indicated on anterior face in American species, absent in some African species 7

2(1). Pronotum longer than wide, its summit less strongly developed; protibia rather broadly flattened, sides parallel, subtruncate apically; xylophagous; USA to Costa Rica; 1.2-2.3 mm .... ***Thysanoes***

— Pronotum as wide or wider than long, summit well developed; protibia slender, weakly or not at all flattened; mostly phloeophagous (some exceptions) 3

3(2). Procoxae contiguous; sutures of antennal club, when present, strongly procurved, suture 1 attaining middle of club; antennal scape short, less than twice as long as club, in female usually as broad as long and ornamented by numerous setae; Africa 4

— Procoxae moderately separated (a few subcontiguous); sutures of antennal club, when present, straight to moderately procurved, never attaining middle of club; scape elongate except subgenus *Aphanocleptus* (*Pseudothysanoes*), its vestiture usually rather sparse; America 6

4(3). Antennal club with sutures present, marked by setae; female mandibular and declivital spines absent; female frons concave to convex; phloeophagous; Madagascar and Africa; 1.1-2.7 mm .... ***Lanurgus***

— Antennal club finely, uniformly, rather densely pubescent, sutures obsolete; female frons concave 5

5(4). Antennal funicle 6-segmented; mandible bearing one or more very long, slender spines directed dorsad; female declivity armed on interstriae 1 at base of declivity by a prominent spine; Africa; 2.2 mm .... ***Traglostus***

— Antennal funicle 5-segmented; mandible normal; declivity unarmed; Africa; 1.3-2.5 mm .... ***Miocryphalus***

6(3). Elytral declivity in both sexes variously sculptured but never sulcate; antennal scape long or short, club with or without sutures; mostly phloeophagous, a few xylophagous; North and South America, 1 in China; 0.7-2.0 mm .... ***Pseudothysanoes***

— Elytral declivity bisulcate, subvertical; antennal scape short, flattened, little if any longer than pedicel, club small, widest through basal half, sutures 1 and 2 straight, indicated by rows of setae; phloeophagous; USA (California) and Mexico (Oaxaca); 1.0-1.5 mm ...... ***Stenoclyptus***

7(1). Eye short, oval, not more than 1.5 times as long as wide (except up to 3.0 times in *Phloeocurus*, Africa), finely faceted; antennal club small, sutures straight to weakly procurved or bisinuate (South American *Hylocurus* with strongly procurved sutures and with posterior face of protibia tuberculate); protibia rather slender, wider apically 8

— Eye elongate, 2.0 or more times as long as wide, coarsely faceted; antennal club rather large, sutures very strongly procurved; protibia rather strongly flattened (posterior face never tuberculate); American species 12

8(7). Antennal club unmarked by sutures, uniformly, finely pubescent, elongate, more than twice as long as wide; female declivity simple, male declivity impressed medially, elevated laterally and armed by large spines; Madagascar; 1.6-2.8 mm .... ***Saurotocis***

— Antennal club stouter, sutures marked by rows of setae 9

9(8). Antennal club with sutures straight, or if bisinuate or procurved, then posterior face of protibia armed by tubercles; American species .. 10

— Antennal club with sutures moderately to profoundly procurved; protibia slender, never armed by tubercles on posterior face; African species 11

10(9). Sutures 1 and 2 on antennal club straight, visible only at margins, obsolete in central area, club small (Fig. 47); protibia entirely unarmed on poosterior face, smooth (Fig. 47); phloeophagous; Mexico; 1.0-1.8 mm ..... ***Phloeocleptus***

— Sutures 1 and 2 on antennal club bisinuate to weakly or strongly procurved, clearly visible in central area of anterior face, club larger; protibia armed on posterior face by many tubercles or rugae; xylophagous; North and South America; 1.3-3.2 mm .... ***Hylocurus***

11(9). Eye larger, more elongate, 2.5-3.0 times as long as wide; sutures of antennal club moderately procurved; protibia slender, with denticles on apical margin; female frons convex; declivity armed by moderately coarse tubercles in both sexes; phloeophagous; Africa; 2.5-3.0 mm .... ***Phloeocurus***

— Eye usually smaller, oval, about twice as long as wide; sutures of antennal club moderately to profoundly procurved, protibia slender, with 1 or more denticles on lateral margin; female frons convex to concave; declivity unarmed; Madagascar, Africa; 1.1-1.8 mm .... ***Pseudomicracis***

12(7). Eye shallowly emarginate, often approximate below; protibia less strongly flattened, at least 1 of 5 apical teeth on outer (lateral) margin; scape usually less strongly expanded; antennal club rather broad, sutures more broadly procurved; monogamous, myelophagous; North America to Colombia; 1.2-2.5 mm .. ***Micracisella***

— Eye entire, always widely separated below; protibia more strongly flattened, all 5 teeth on apical margin; scape usually very strongly expanded; antennal club more elongate, sutures usually much more strongly, narrowly arcuate; bigynous, xylophagous; North and South America; 1.6-3.4 mm .... ***Micracis***

Lanurgus **Eggers** [1920a: 36, Type-species: *Lanurgus barbatus* Eggers, monobasic. Synonyms: *Landolphianus* Schedl 1950c: 106, Type-species: *Landolphianus elongatus* Schedl, subsequent designation by Schedl 1962a: 38; *Micraciops* Schedl 1953a: 86, Type-species: *Micraciops catenatus* Schedl, subsequent designation by Schedl 1962: 38; *Pseudohylocurus* Nunberg 1961: 613, Type-species: *Pseudohylocurus caplandicus* Nunberg =*Lanurgus podocarpi* Schedl, original designation]. Distribution: 24 species in Africa and Madagascar.

Traglostus **Schedl** [1938d: 454, Type-species: *Traglostus exornatus* Schedl, monobasic]. This genus is doubtfully distinct from *Lanurgus*. Distribution: 4 species from Kenya to South Africa.

Miocryphalus **Schedl** [1939d: 381, Type-species: *Stephanoderes natalensis* Eggers, monobasic. Synonym: *Afromicracis* Schedl 1959d: 709, Type-species: *Afromicracis kenyaensis* Schedl, monobasic]. Distribution: 6 species in Africa.

Pseudothysanoes **Blackman** [1920: 46, Type-species: *Pseudothysanoes drakei* Blackman =*Cryphalus rigidus* LeConte, original designation. Synonyms: *Cryptocleptes* Blackman 1920: 51, Type-species: *Cryptocleptes dislocatus* Blackman, original designation, preoccupied; *Chalcohyus* Blackman 1943b: 363, Type-species: *Chalcohyus securigerus* Blackman, original designation; *Bostrichips* Schedl 1951a: 21, Type-species: *Bostrichips spinatus* Schedl, monobasic; *Gretschkinia* Sokanovskii 1959: 276, Type-species: *Gretschkinia mongolica* Sokanovskii, mono-basic; *Aphanocleptus* Wood 1960b: 63, Type-species: *Aphanocleptus coniferae* Wood, original designation; *Cryptulocleptus* Wood 1962: 76, Type-species: *Cryptocleptes dislocatus* Blackman, automatic; *Neoglostatus* Schedl 1978:

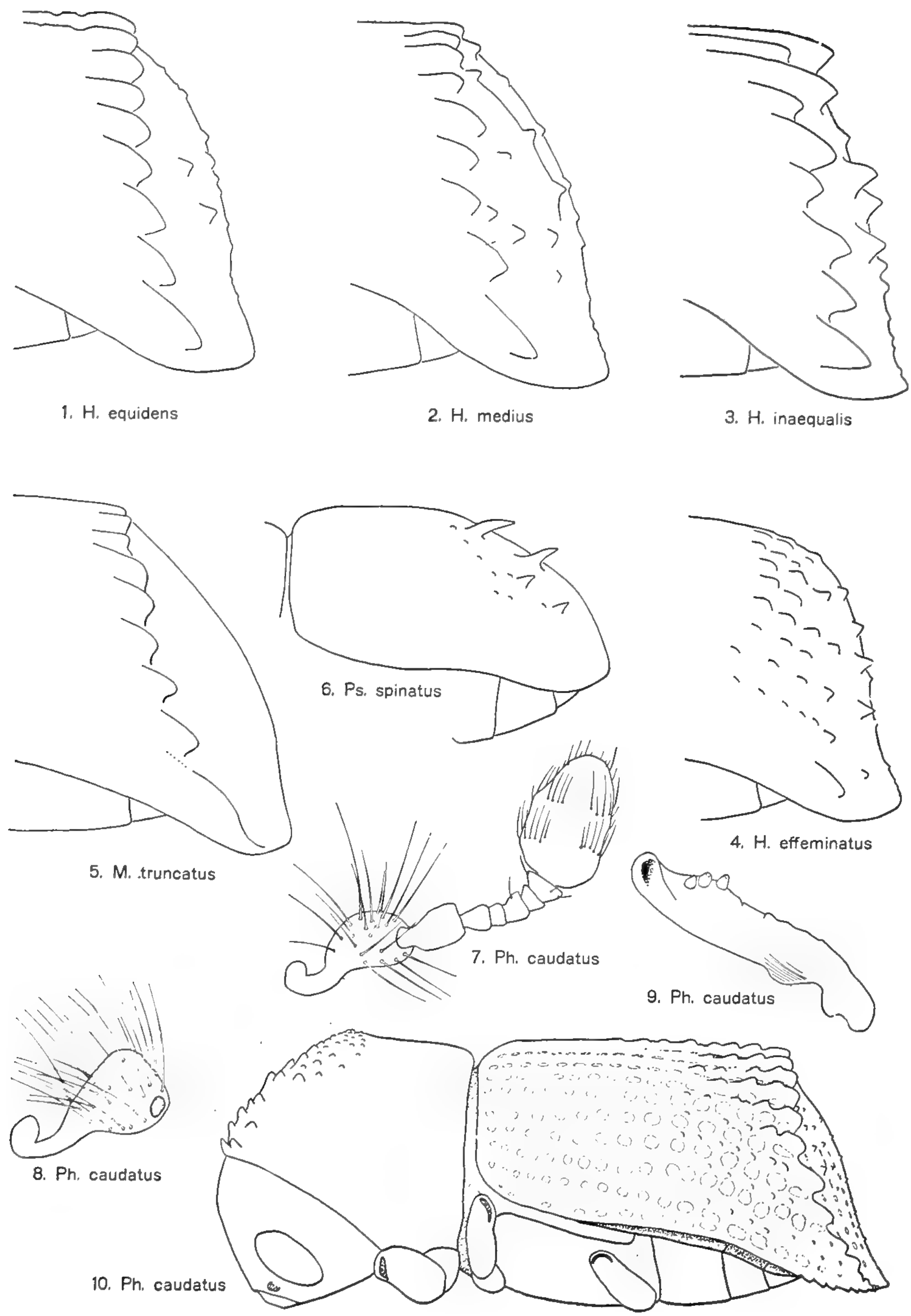


Fig. 47. Micracini spp., elytral declivities, antennae, and protibia: 1, *Hylocurus equidens* Wood, male; 2, *Hylocurus medius* Wood, male; 3, *Hylocurus inaequalis* Wood, male; 4, *Hylocurus effeminatus* Wood, male; 5, *Micracis lignator* Blackman (= *truncatus* Wood), male; 6, *Pseudothysanoes spinatus* Wood, male; 7-10, *Phloeocleptus caudatus* Wood, 7, 10, male, 8, 9, female.

300, Type-species: *Neoglostatus squamosus* Schedl, monobasic]. Distribution: 61 species in North and Central America, 8 in the Antilles Islands and South America, 1 in China. All are bigynous; most are phloeo-phagous, a few (about 6) are xylophagous, a few bore in leaves, etc. Key: Wood (1982: 511) for North and Central America.

Stenoclyptus **Blackman** [1943b: 356, Type-species: *Stenoclyptus rhois* Blackman = *Pseudothysanoes sulcatus* Bruck, original designation]. Distribution: 2 species in USA (California) to Mexico (Puebla). Both are bigynous and phloeophagous. Key: Wood (1982: 556).

Saurotocis **Wood** [1984: 229, Type-species: *Micracidendron tomicoides* Schedl, original designation]. Distribution: 2 species in Madagascar.

Thysanoes **LeConte** [1876: 369, Type-species: *Thysanoes fimbricornis* LeConte, monobasic]. Distribution: 13 species in USA to Costa Rica. Key: Wood (1982: 557).

Phloeocleptus **Wood** [1956a: 147, Type-species: *Phloeocleptus caudatus* Wood, original designation]. Distribution: 11 species from North America (Mexico) to Central America (Costa Rica). All are bigynous and phloeophagous. Key: Wood 1982: 570).

Hylocurus **Eichhoff** [1872: 133, Type-species: *Hylocurus elegans* Eichhoff, monobasic. Synonym: *Micracisoides* Blackman 1920: 19, Type-species: *Micracis rudis* LeConte, subsequent designation by Wood 1982: 608]. Distribution: 34 species in North and Central America, about 20 in South America and adjacent islands. All are bigynous and xylophagous. Keys: Blandford (1898: 220), Wood (1982: 609).

Phloeocurus **Wood** [1984: 230, Type-species: *Hylocurus africanus* Schedl, original designation]. Distribution: 1 species in Africa.

Pseudomicracis **Eggers** [1920a: 36, Type-species: *Pseudomicracis elsae* Eggers, monobasic]. Although the unique holotype of the type-species is lost, the genus is identifiable from the description. Distribution: 7 species in Africa and Madagascar.

Micracisella **Blackman** [1928b: 192, Type-species: *Micracis opacicollis* LeConte, automatic. Synonym: *Pseudomicracis* Blackman 1920 (December): 20, Type-species: *Micracis opacicollis* LeConte, original designation, preoccupied]. Distribution: 20 species in North and Central America 1 of which also occurs in South America (Colombia). All are monogamous and myelophagous. Key: Wood (1982: 594).

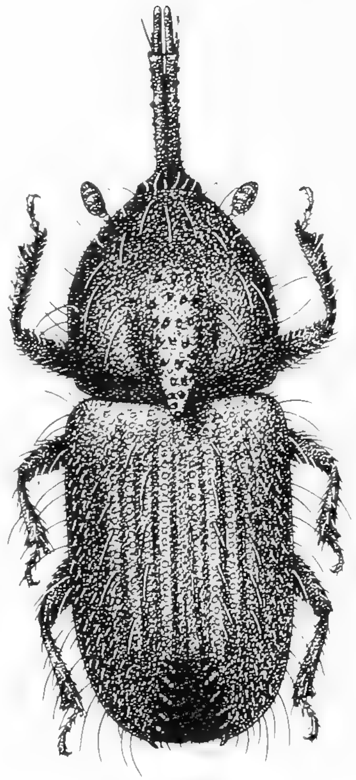


Fig. 48. *Cactopinus desertus* Bright, male. (After Bright 1973: 155).

Micracis **LeConte** [1868: 164, Type-species: *Micracis suturalis* LeConte, subsequent designation by Hopkins 1914: 125]. Distribution: 18 species in North and Central America, 1 in Cuba, 2 in South America (Venezuela); several others have been named from South America but most, if not all of these, have been or should be transferred to other genera. All are bigynous and xylophagous. Key: Wood (1982: 579).

Tribe Cactopinini

Cactopinae Chamberlin [1939: 243, Type-genus: *Cactopinus* Schwarz, 1899]

DESCRIPTION.—Frons dimorphic, male strongly impressed or excavated, with the epistomal margin armed by a pair of (usually

confluent) hornlike spines of large to enormous size (Fig. 48), female convex or modestly impressed, epistoma unarmed by spines; posterodorsal area of head modestly produced caudad; eye small, oval, entire; antennal scape rather short, funicle 5-segmented, club almost conical to strongly flattened, sutures straight to procurved, marked by rows of setae; pronotum asperate on anterior slope, summit at or near posterior margin, sometimes projecting caudad beyond basal margin; procoxae contiguous; elytral sculpture unique, rather conservative, usually sulcate on declivity, almost always coated by resinous film of host origin.

BIOLOGY.—All are monogamous and either phloeophagous or in cactus (*Cereus* and allied genera). Those in cactus breed in dry, dead (yellowing) tissue immediately below the epidermis, or in scar tissue in deep wounds (*hubbardi*). One species breeds in *Yucca* leaves (*depressus*). The parental galleries form an irregular cave, with egg niches. Eggs are deposited individually in niches in two species; some species in cactus deposit them in clusters. Larval mines may be individual or lost in a criss-crossing maze. Successive generations have been bred in the same piece of dry cactus for four years. Symbiotic relationships with fungi have not been reported.

TAXONOMY.—This unique tribe is restricted to the Mexican plateau region. Its nearest affinity to other groups appears to be with the Micracini, although the relationship is remote. They are exceedingly rare.

***Cactopinus* Schwarz** [1899: 11, Type-species: *Cactopinus hubbardi* Schwarz, monobasic. Synonym: *Cactopinorus* Bright 1967: 918, Type-species: *Cactopinus cactophthorus* Wood, original designation]. Distribution: 19 species in W North America (California and W Utah to Mexico). All are monogamous and phloeophagous when in woody plants or subepidermal when in cactus (*Cereus* and allied genera only). Keys: Blackman (1938a: 151), Bright (1967: 919), Wood (1969: 43, 1982: 638).

Tribe Carphodicticini

Carphodicticini Wood [1971: 19, Type-genus: *Carphodicticus* Wood, 1971]

DESCRIPTION.—Frons weakly to moderately dimorphic, male strongly convex, female slightly to moderately flattened and sometimes abundantly pubescent; eye short, broadly oval and entire to very elongate and sinuate to shallowly emarginate; scape short and rather stout to elongate and rather slender, funicle 5-segmented, club flattened, small, and symmetrical, with transverse sutures, to moderately large and slightly asymmetrical, with slightly oblique sutures, sutures marked by grooves and rows of setae, apparently not septate; pronotum elongate, sides conspicuously constricted on middle half, pronotum unarmed; posterior face of head truncate, dorsomedian area not extended caudad; procoxae narrowly to rather widely separated; protibia slender to very stout and short, armed by socketed denticles on lateral margin; scutellum visible; basal margins of elytra rounded in two genera, elevated and carinate in one genus.

BIOLOGY.—*Carphodicticus* is monogamous and phloeophagous. Numerous pairs of parent adults appeared to use the same entrance tunnel. Each pair followed a previously made tunnel for a short distance, then formed their own branch gallery for oviposition, such that the entire system consisted of branching and rebranching galleries. Eggs were deposited individually in niches at the cambium. Larval mines were exposed on peeled bark and were rather short. The host had been felled for several months before this species attacked; a *Phloeotribus* had largely abandoned the unusually hot, dry tissues, but this species was thriving.

TAXONOMY.—The head and pronotal structure suggest that this group is very primitive. It was probably derived from the same ancestral stock as the Dryocoetini, Ipini, Crypturgini, Xyloterini and Xyleborini, but at a much earlier date. The disjunct distribution and rarity suggest that it is a relict group that had reached its maximum potential prior to the Tertiary. This tribe represents a first step toward one of the three most hightly evolved tribes (Xyleborini) of Scolytidae.

Key to the Genera of Carphodicticini

1. Eye entire, broadly oval, short, about 1.3 times as long as wide; scape rather short, about three times as long as pedicel; antennal club rather small, sutures transverse; elytral apex strongly mucronate; ventrolateral margin of declivity armed by a row of rather strongly elevated serra-

armed by a row of rather strongly elevated serrations; apparently xylophagous; India and Sri Lanka (Ceylon); 1.3-2.3 mm ...... *Craniodicticus*

— Eye sinuate to emarginate, elongate, more than twice as long as wide (not visible on type of *Dendrodicticus*); elytral apex rounded, not mucronate; lateral margin of declivity uniformly elevated, not armed by serrations 2

2(1). Basal margins of elytra rounded, not elevated; antennal club rather large, distinctly asymmetrical, sutures slightly oblique; procoxae more narrowly separated; protibia short (only slightly longer than antennal club), stout (almost half as wide as long); phloeophagous; South America (Venezuela); 2.0-2.4 mm .... *Carphodicticus*

— Basal margins of elytra rather strongly, acutely elevated along a continuous costa; antennal club rather small, symmetrical, sutures transverse; procoxae more widely separated; protibia longer, much more slender; habits unknown; South America (Argentina); 2.0 mm .... *Dendrodicticus*

***Craniodicticus* Blandford** [1895: 317, Type-species: *Craniodicticus mucronatus* Blandford, monobasic]. Distribution: 1 species in S India, 1 in Sri Lanka (Ceylon). They apparently are xylophagous, since one sample was "removed from wood" and the other from a creeper called "jungle rope."

***Carphodicticus* Wood** [1971: 19, Type-species: *Carphodicticus cristatus* Wood, original designation]. Distribution: 1 species in South America (Venezuela). It is monogamous and phloeophagous; it utilized the entrance tunnels of a *Phloeotribus* species in order to gain access to the phloem.

***Dendrodicticus* Schedl** [1958a: 37, Type-species: *Dendrodicticus argentiniae* Schedl, monobasic]. Distribution: 1 species in South America (Argentina).

Tribe Ipini

Ipini Bedel [1888: 386, Type-genus: *Ips* DeGeer, 1775]

DESCRIPTION.—Frons usually dimorphic, male convex, female variously excavated, protuberant, or ornamented by setae; eye sinuate, lower half usually much narrower than above; antennal scape slender, elongate, funicle 5-segmented, club either obliquely truncate or sutures on posterior face strongly displaced toward apex; pronotum rather strongly declivous on anterior half, rather closely, coarsely asperate; procoxae contiguous, intercoxal piece deeply notched or absent; protibia armed by three or four socketed teeth; scutellum visible; elytral declivity moderately sulcate to strongly excavated, lateral margins usually armed by tubercles or spines; vestiture hairlike.

BIOLOGY.—All are phloeophagous. Most are heterosanguineously polygynous, although some *Acanthotomicus* are monogamous. Hosts include members of the Pinaceae, except *Acanthotomicus* breeds primarily in various angiosperm trees. Eggs are deposited in niches. Larval mines are individual and rarely cross one another; they are exposed on the surface of peeled bark. The life cycle is comparatively short, with two or more generations per year apparently the normal habit.

TAXONOMY.—In most tribes of Scolytidae the sexes are easily distinguished by a difference in the number of abdominal terga. The female tergum 8 is reduced in size and is telescoped beneath tergum 7 such that it is ordinarily hidden from view. A visible tergum 8 is present in the male. However, in Carphodicticini, Ipini, Dryocoetini, Crypturgini, Xyloterini, and Xyleborini a small tergum 8 is visible in both sexes. The general body habitus, shape of the eye, basic type of antennal club (trend toward being obliquely truncate), and tibiae are also shared by these tribes. The Ipini occupy a position between Carphodicticini and Dryocoetini in which these characters were being formed. In *Dendrochilus* they are so poorly expressed that they are detected only with difficulty. However, that genus does exhibit a stage in transition to the circumtropical *Acanthotomicus*.

Acanthotomicus appears to have an ancient origin (prior to the Tertiary) and to have given rise, directly or indirectly, to *Pityogenes*, *Pityokteines*, *Orthotomicus*, and *Ips*. *Pityogenes* appears to have arisen in Europe and northern Asia from African *Acanthotomicus*-like stock and to have reached North America rather recently. Something resembling the neotropical *Acanthotomicus mimicus* species group probably gave rise in North America in early Tertiary to a stock that then evolved into *Pityokteines* and *Ips* in North America and to *Orthotomicus* in Europe and Asia. At a later date, a few representatives of *Pityokteines* and *Ips* then migrated into Europe and Asia and one species of *Orthotomicus* reached North America. The reasoning on which the above is

based is (1) on the continent of origin of several species groups found today, only a fractional number of those species groups now occur in the invaded territory and (2) no species group is found in the invaded territory that is not presently also found in the area of origin. Fossils that might document this supposition are unknown. *Dendrochilus* and *Acanthotomicus* breed in a variety of nonconiferous hosts; *Pityogenes, Pityokteines, Orthotomicus*, and *Ips* occur exclusively in Pinaceae.

Key to the Genera of Ipini

1. Eye short, oval, entire, not sinuate on anterior margin; antennal club rather small, flattened, unmarked by sutures; declivity convex to slightly, broadly flattened, without granules or tubercles; elytral vestiture not abundant, in rows, interstrial setae hairlike to scalelike; protibia slender, armed by 3 socketed denticles on apical half of lateral marin; Africa; 1.0-2.0 mm .... *Dendrochilus*
— Eye more elongate, sinuate on anterior margin; antennal club usually larger, marked by sutures (except absent in many *Acanthotomicus*); declivity usually excavated and variously armed by tubercles or spines 2

2(1). Elytral declivity rather narrowly bisulcate, lateral margins rather broadly elevated, rounded, and armed by not more than 3 pairs of denticles; lower margin of declivity rounded; usually smaller than 3 mm 3
— Elytral declivity broadly, rather deeply excavated, margins acutely elevated and armed by 3 or more pairs of denticles (1 to 6 pairs in tropical *Acanthotomicus*); lower margin of declivity with an acutely elevated, transverse ridge separating declivital excavation from apical margin (Fig. 49); usually larger than 3 mm 4

3(2). Prosternal intercoxal piece short, obtuse; female frons sometimes deeply, rather narrowly excavated; male declivity with 2 or 3 pairs of enlarged denticles; antennal club compressed, 2 sutures visible on apical third of posterior face; North America, Europe, Asia, N Africa; Pinaceae; 1.8-3.7 mm .... *Pityogenes*
— Prosternal intercoxal piece long and acutely tapered; female frons convex, never excavated; male declivity more narrowly impressed; female frons and anterior pronotum with dense, long vestiture (2 American exceptions); North America, Asia, Europe; *Abies*; 1.6-3.0 mm .... *Pityokteines*

4(2). Antennal club obliquely truncate, sutures recurved; third (lowest) major denticle not on lateral margin of elytral declivity, displaced mesad from margin; eye of normal size; North America, Asia, Europe; Pinaceae; 2.2-4.3 mm .... *Orthotomicus*
— Antennal club flattened, sutures either procurved or moderately to strongly bisinuate; lateral margins of elytral declivity armed by 1 to 6 pairs of major denticles, third pair (if present) on or incorporated into crest of lateral margin; eye usually either abnormally large or else very small 5

5(4). Sutures of antennal club (when present) moderately to very strongly procurved; eye large, very coarsely faceted, its width about equal to length of scape, its length more than twice length of scape; Mexico to South America, S Asia to Australia, Africa; angiosperm hosts (some Asian exceptions); 1.4-2.7 mm .... *Acanthotomicus*
— Sutures of antennal club moderately to strongly bisinuate (procurved in *concinnus, mexicanus, orientalis*); eye small, finely faceted, its width equal to much less than length of scape, its length equal to much less than twice length of scape; North America to N Nicaragua, Asia, Europe, N Africa; Pinaceae; 2.1-6.9 mm .... *Ips*

***Dendrochilus* Schedl** [1957a: 70, Type-species: *Dendrochilus strombosiopsis* Schedl, subsequent designation by Schedl 1962a: 55]. Distribution: About 10 species from Africa.

***Pityogenes* Bedel** [1888: 397, Type-species: *Dermestes chalcographus* Linnaeus, original designation. Synonyms: *Eggersia* Lebedev 1926: 121, Type-species: *Bostrichus bidentatus* Herbst, present designation; *Pityoceragenes* Balachowsky 1947: 44, Type-species: *Bostrichus quadridens* Hartig, original designation]. Distribution: 7 species in North America, 18 in Europe, Asia, and N Africa. All are heterosanguineously polygynous and phloeophagous. Keys: Swaine (1918: 104), Bright (1976: 150), and Wood (1982: 650) for North America, Reitter (1913: 97) and Pfeffer 1946: 112) for Europe, Stark (1952: 272) for USSR, Schedl (1962c: 134) for Europe and Asia.

***Pityokteines* Fuchs** [1911: 33, Type-species: *Ips curvidens* Germar, subsequent designation by Hopkins 1914: 127. Synonymy: *Orthotomides* Wood 1951: 32, Type-species: *Orthotomicus lasiocarpi* Swaine, original designation]. Distribution: 6 species in North America, 3 in Asia and Europe. All are heterosanguineously polygynous and phloeophagus. Keys: Swaine (1918: 123), Bright (1976: 145), and Wood (1982: 656) for North America, Reitter (1913: 102) for Europe, Balachowsky (1949: 255) for France, Stark (1952: 421) for the USSR.

***Orthotomicus* Ferrari** [1867: 44, Type-species: *Bostrichus laricis* Fabricius, subsequent

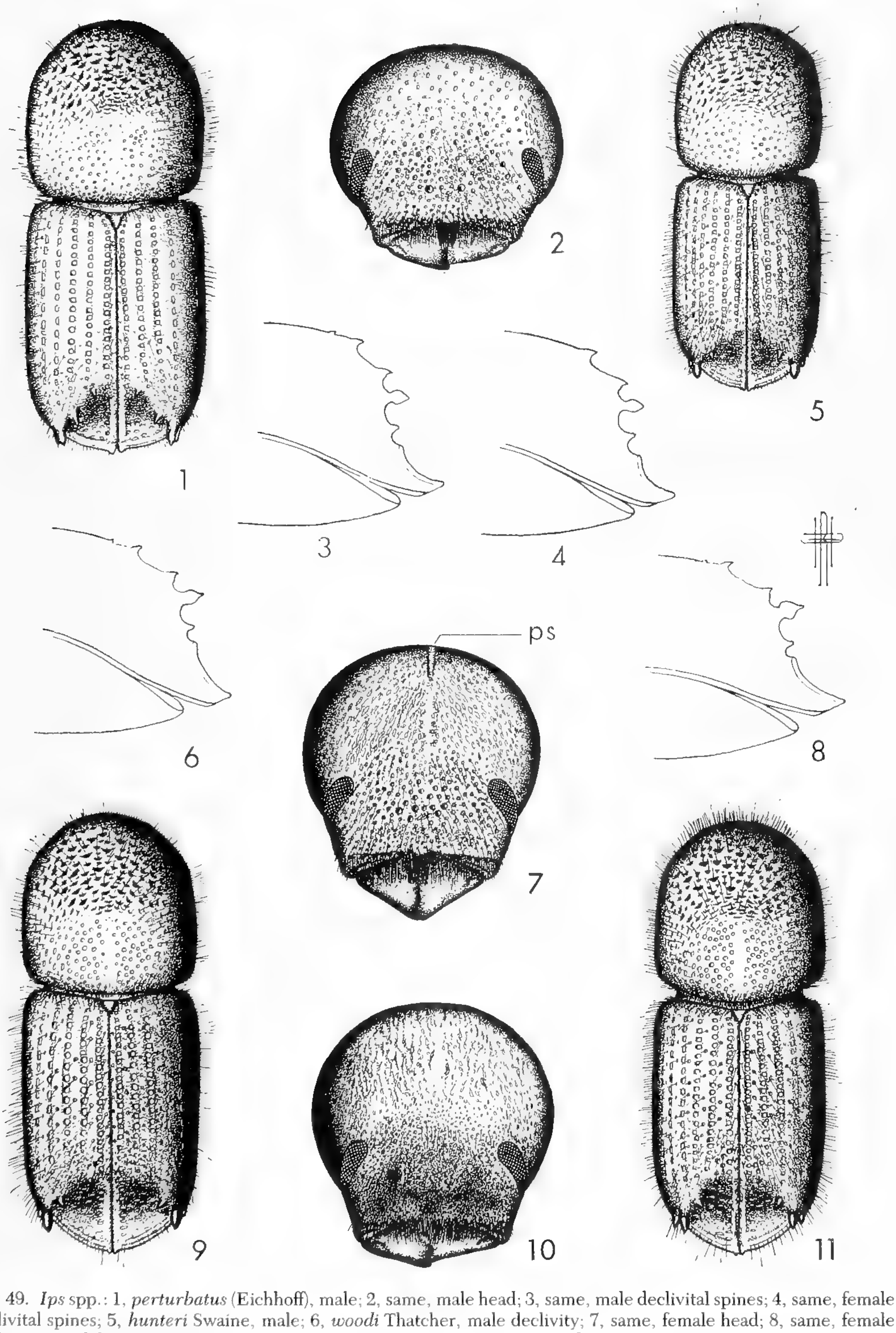


Fig. 49. *Ips* spp.: 1, *perturbatus* (Eichhoff), male; 2, same, male head; 3, same, male declivital spines; 4, same, female declivital spines; 5, *hunteri* Swaine, male; 6, *woodi* Thatcher, male declivity; 7, same, female head; 8, same, female declivity; 9, *pilifrons utahensis* Wood, male; 10, same, female head; 11, *woodi*, female. (After Hopping 1965: 536).

designation by Hopkins 1914: 126, original spelling *Onthotomicus* Ferrari (1867: 44), a lapsus calami that was corrected by Ferrari (1869: 256). Synonym: *Neotomicus* Fuchs 1911: 33, Type-species: *Bostrichus laricis* Fabricius, subsequent designation by Hopkins 1914: 125]. Distribution: 1 species in North America, about 10 in Asia, Europe, and N Africa. All are heterosanguineously polygynous and phloeophagous. Keys: Reitter (1913: 108) for Europe, Balachowsky (1949: 268) for France, Stark (1952: 407) for the USSR.

***Acanthotomicus* Blandford** [1894a: 89, Type-species: *Acanthotomicus spinosus* Blandford, monobasic. Synonym: *Mimips* Eggers 1932: 33, Type-species: *Ips pilosus* Eggers, original designation; *Isophthorus* Schedl 1938c: 173, Type-species: *Isophthorus quadrituberculatus* Schedl, designated by Wood 1980: 89]. Distribution: 10 species in Central and South America, more than 20 in Africa and about 14 in China and Japan to Australia and the Philippines. All are phloeophagous; of 13 species studied in nature by me, 1 was monogamous and 12 heterosanguineously polygynous. Key: Wood (1982: 664) for Central America.

***Ips* DeGeer** [1775: 190, Type-species: *Tomicus typographus* =*Dermestes typographus* Linnaeus, subsequent designation by Bergroth 1884: 230. Synonyms: *Cumatotomicus* Ferrari 1867: 44, Type-species: *Bostrichus stenographus* Duftschmidt =*Dermestes sexdentatus* Boerner, subsequent designation by Hopkins 1914: 119; *Cyrtotomicus* Ferrari 1867: 44, Type-species: *Bostrichus acuminatus* Gyllenhal, subsequent designation by Hopkins 1914: 120]. Distribution: 25 species in North and Central America, about 18 in Asia, Europe, and N Africa; at least 1 has been introduced to Australia and the Philippine Islands. All are heterosanguineously polygynous and phloeophagous. Numerous species belonging to other genera have erroneously been assigned to this genus at one time or another. Keys: Schedl (1950b: 69) for Europe and Asia, Hopping (1963-1965) and Wood (1982: 669) for North and Central America.

Tribe Dryocoetini

Dryocoetoideae Lindemann [1876: 165, Type-genus: *Dryocoetes* Eichhoff, 1864]
Thamnurginae Nüsslin [1911: 377, Type-genus: *Thamnurgus* Eichhoff, 1864]
Taphrorychini Reitter [1913: 29, Type-genus: *Taphrorychus* Eichhoff, 1878]

DESCRIPTION.—Frons usually sexually dimorphic, male convex to variously impressed, female convex to flattened or with elevations, variously ornamented by setae in many species; eye distinctly emarginate to divided; antennal scape slender, elongate, funicle 4- to 6-segmented, club obliquely truncate to strongly flattened, if flattened then sutures variously procurved to obsolete, and, on posterior face, strongly displaced toward apex; pronotum arched from base or not, if anteriorly declivous then declivity usually involving more than anterior half, armed or not, if armed then asperities small, usually abundant; procoxae contiguous to narrowly separated; protibia with lateral margin armed by four to several socketed teeth (*Chiloxylon* and a few *Coccotrypes* have three); scutellum visible; elytral declivity usually convex, sometimes shallowly sulcate or variously flattened, sometimes armed by small granules; vestiture hairlike.

BIOLOGY.—Apparently all are polygynous, with heterosanguineous polygyny occurring in all except the consanguineous *Dryocoetiops*, *Coccotrypes* (Fig. 50), and *Ozopemon*. Most are phloeophagous, *Dactylotrypes* and some *Coccotrypes* are spermophagous, and at least one species (*Dryocoetiops coffeae*) is myelophagous. Most eggs are placed in individual niches. Most larvae form independent mines, but some feed in congress.

TAXONOMY.—This is a large, rapidly evolving group; consequently, generic boundaries are not always clear. Three major groups of genera are apparent: (1) *Dryocoetiops*, *Coccotrypes*, and *Ozopemon*, (2) *Dactylotrypes*, *Dendrocranulus*, *Xylocleptes*, *Thamnurgus*, *Tiarophorus*, *Triotemnus*, etc., and (3) *Cyrtogenius*, *Dryocoetes*, *Lymantor*, etc.

Although structural diversity may not warrant it, these three species groups will be discussed separately. In group 1, reproduction in all species involves arrhenotocous parthenogenesis. Males, if known, are dwarfed, deformed, flightless, and haploid. With about two possible American exceptions in *Coccotrypes*, all species originally occurred in the Ethiopian, Oriental, or Australian realms. Many spermophagous *Coccotrypes* have been transported through

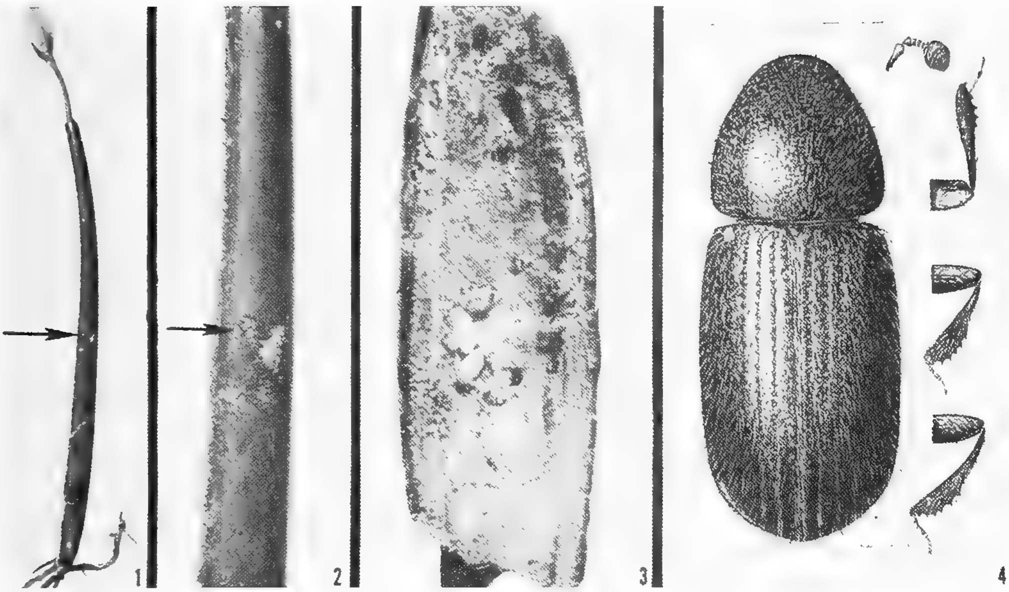


Fig. 50. *Coccotrypes rhizophorae* Hopkins: 1, entrance tunnel in *Rhizophora mangle* seedling; 2 and 3, larvae in host stem; 4, adult female. (After Woodruff 1970: 1).

commerce far beyond their original geographical distributions. Of the dozen or so American species, all but two are known to have reached America through commerce, and it is presumed that in time these two will be found to have foreign origins.

Group 2 is one of the few scolytid groups to invade herbaceous plants (mostly Cucurbitaceae and Euphorbiaceae). A thorough study of *Thamnurgus*, *Xylocleptes*, and *Taphronurgus* will probably find that intergradation between them is complete and, consequently, that they must be combined into one genus. Group 2 undoubtedly is the most ancient of this tribe. If *Dendrocranulus* (American) was separated from the almost indistinguishable *Xylocleptes* (African) by early Tertiary, then the origin of their common ancestor and of the tribe must be pushed back into the Cretaceous. Early members of this group probably gave rise to groups 1 and 3.

Group 3 appears to have originated in the Old World, with *Dryocoetes* and *Lymantor* reaching northern North America rather recently. Schedl repeatedly called attention to the similarity between some of the small, slender *Cyrtogenius* and *Pityophthorus*; however, the antennae, elytral locking mechanism, and other characters are so totally different that there is no possibility of a close relationship between these groups.

Key to the Genera of Dryocoetini

1. Protibia armed on lateral margin by 5 or more socketed teeth (rarely 1 or 2 reduced, if so, then sutures on anterior face of antennal club procurved, except only 2 teeth present in *Dolurgocleptes*); posterior face of antennal club with only one suture indicated (except 2 in some *Taphrorychus*), sutures on anterior face either procurved or club obliquely truncate, suture 1 more commonly on apical half; male of normal size, joins female in new parental gallery 2

— Protibia armed on lateral margin by 2 to 4 socketed teeth; posterior face of antennal club marked by 2 sutures, suture 1 on anterior face usually on basal third, both sutures either straight or recurved; lateral margins of pronotum usually acutely or subacutely elevated at least near base (some exceptions); male dwarfed, of abnormal shape, flightless, never joins female in new parental gallery (except unknown in *Chiloxylon*) 15

2(1). Antennal funicle 4- or 6-segmented; pronotum unarmed, feebly if at all declivous on less than anterior fourth; eye deeply emarginate to divided; male frons moderately to strongly impressed 3

— Antennal funicle 2- to 5-segmented; anterior half of pronotum declivous and armed by asperities (except feebly declivous and unarmed in *Thamnurgus*) 5

3(2). Antennal funicle 6-segmented; pronotum conspicuously longer than wide, feebly declivous on less than anterior half; sutures on antennal club procurved; procoxae narrowly separated; Africa; Euphorbiaceae; 1.4-5.5 mm .... ***Tiarophorus***

— Antennal funicle 4-segmented, sutures of club straight or slightly recurved (when present); pronotum feebly to moderately declivous on more than anterior third; procoxae contiguous 4

4(3). Eye divided; protibia rather broad, margin with only 2 socketed teeth; antennal club membranous and pubescent, with 1 suture indicated at middle on front and back; pronotum smooth, shining throughout, very feebly declivous on anterior half; striae not impressed, punctures small, in rows, scarcely larger than those of interstriae; Madagascar; 1.9 mm .... ***Dolurgocleptes***

— Eye sinuate on anterior margin; lateral margin of protibia armed by 4 or 5 socketed teeth; strial punctures usually larger, deeper, distinctly larger than those of interstriae; Africa to India; *Euphorbia*; 1.2 mm ...... ***Triotemnus***

5(2). Protibia more broadly flattened on at least apical half, lateral margin armed by 7 or more socketed teeth; male frons variously impressed, female flat to convex and ornamented or not; sutures on antennal club modestly to profoundly procurved, except recurved in some *Thamnurgus*; scutellum very small, not flat; in stems of Cucurbitaceae or Euphorbiaceae 6

— Protibia less strongly flattened on apical third, lateral margin armed by 5 socketed teeth (rarely 3 to 6); male frons convex (rarely feebly impressed), female variously modified and frequently ornamented by hair; sutures on antennal club recurved, straight, procurved, or obsolete; scutellum rather large, flat; in phloem or xylem of trees and shrubs 10

6(5). Groove on posterior face of metatibia for reception of tarsus poorly developed, short, occupying less than apical third; Europe and Asia to Africa 7

— Metatibial groove conspicuous, occupying more than apical three-fourths on posterior face; America and Canary Islands 9

7(6). Pronotum less distinctly declivous on anterior third, punctured to anterior margin, margins of some punctures feebly to finely asperate; antennal club rather small, sutures straight to recurved; male frons feebly impressed; Europe and SW Asia to N Africa; mostly in Euphorbiaceae; 2.0-3.0 mm .... ***Thamnurgus***

— Anterior third of pronotum finely asperate, punctures obsolete in asperate area 8

8(7). Antennal club shorter than scape, 1.3 times as long as wide, sutures weakly procurved; male frons rather strongly impressed; SE Europe; *Clematis*; 1.8-2.0 mm .... ***Taphronurgus***

— Antennal club distinctly longer than scape, more broadly rounded, sutures rather weakly to very strongly procurved; male frons indistinctly impressed; S Europe, Africa; Cucurbitaceae, etc.; 2.0-2.7 mm .... ***Xylocleptes***

9(6). Sutures of antennal club obscure, strongly procurved, basal area of club not corneous; body more slender, pronotum with asperities usually restricted to anterior half; America; Cucurbitaceae; 1.2-2.7 mm .. ***Dendrocranulus***

— Sutures of antennal club on apical fourth, recurved, basal three-fourths of club thickened, corneous; body rather stout; asperities extend to base of pronotum; Canary Islands; *Dracaena draco*; 1.8-2.0 mm ...... ***Dactylotrypes***

10(5). Antennal funicle 4-segmented, sutures of club very strongly procurved; male frons shallowly to moderately impressed, female frons less distinctly impressed; slender species with punctures on elytral disc confused; partly xylophagous; North America, N Asia, Europe; 1.6-2.0 mm .... ***Lymantor***

— Antennal funicle 5-segmented (rarely 2-, 3-, or 4-segmented in New Guinea and Indonesia species), sutures on club procurved or not; male frons usually convex, female frons frequently pubescent 11

11(10). Pronotum with summit distinctly elevated near middle, often a moderate, transverse impression behind summit; antennal club strongly flattened, basal area slightly corneous, suture 1 distinct, straight to strongly bisinuate, its lateral extremities reaching basal fourth, median portion never exceeding middle of club, 2 sutures on posterior face; meso- and metatibiae more slender; hair on pronotum and elytra fine, unusually long; Europe and Asia; broadleaf hosts; 1.8-3.2 mm .... ***Taphrorychus***

— Pronotum with dorsal profile evenly arched, summit inconspicuous or else on basal fourth; basal area of antennal club less strongly flattened, more strongly corneous or if not corneous then sutures obsolete and pubescence extending to base; meso- and metathoracic tibiae usually more broadly flattened; pronotal and elytral setae of more normal length .. 12

12(11). Antennal funicle 2-segmented, procurved corneous area of club occupying more than three-fourths of basal area; procoxae contiguous; New Guinea to New Britain Island; 1.2-1.4 mm .... ***Dendrographus***

— Antennal club 3-, 4-, or 5-segmented; usually much larger 13

13(12). Body very stout, 2.0-2.1 times as long as wide; pronotum rather coarsely asperate to base, summit on basal fourth; antennal club either devoid of sutures or with 1 on basal fourth, almost straight except recurved at margins; procoxae narrowly separated; declivity strongly arched, convex, apical fourth exceeding vertical and slightly undercutting central

area; New Guinea to Borneo; 1.6-1.8 mm . . . . ***Peridryocoetes***

— Body more slender; pronotum usually with punctures on at least part of basal half, summit indefinite, not on basal fourth 14

14(13). Antennal club with suture 1 weakly to profoundly procurved, rarely with sutures absent and pubescent to base; funicle of small species with as few as 3 segments (most 4- or 5-segmented); procoxae narrowly separated, rarely intercoxal piece longitudinally emarginate; commonly with ventrolateral margin of declivity slightly elevated or armed; Micronesia to Africa; mostly non-coniferous hosts; 1.3-3.0 mm . . . . ***Cyrtogenius***

— Antennal club with suture 1 recurved, always present, never pubescent to base; procoxae contiguous, intercoxal piece always longitudinally emarginate or absent; ventrolateral margin of declivity never acutely elevated or specially armed; North America, Asia, Europe, N Africa; mostly coniferous hosts; 1.5-5.1 mm . . . . ***Dryocoetes***

15(1). Protibia rather broad apically, lateral apical angle abrupt (almost 90 degrees), 1 denticle on this angle, another on apical margin, and a third on lateral margin one-fourth tibia length from apical angle; funicle 4-segmented, club constricted at partly septate suture 1 (not actually obliquely truncate), suture 2 indicated by setae; habitus resembling *Dryocoetes*, uniseriate interstrial setae almost scalelike on declivity, declivity very steep; strial punctures coarse, deep; Brazil; 1.7 mm . ***Chiloxylon***

— Protibia narrowed near apex, outer apical angle not abrupt; funicle 4-segmented, club never septate, obliquely truncate or nearly so 16

16(15). Procoxae narrowly to moderately separated; anterior margin of pronotum usually armed by serrations (absent in some *laevis*); pronotum usually more coarsely asperate in anterior areas, its summit more definite and near middle; India and Sri Lanka (Ceylon) to Philippines; broadleaf hosts; 1.7-3.5 mm . . . . ***Dryocoetiops***

— Procoxae contiguous, intercoxal piece either longitudinally notched or absent; anterior margin of pronotum unarmed, pronotum usually more finely asperate to unarmed anteriorly, its summit less definite and usually well behind middle 17

17(16). Lateral margins of pronotum obscurely to subacutely elevated only near base; frons never convergently aciculate; anterior half of pronotum always strongly declivous and asperate; elytral declivity either moderately impressed on central half and with interstrial tubercles or discal punctures strongly confused; mesocoxae subcontiguous, separated by distance equal to width of antennal pedicel; phloeophagous; Indonesia and Malaya to Fiji; broadleaf hosts; 3.3-5.5 mm . . . . ***Ozopemon***

— Lateral margins of pronotum subacutely elevated on more than basal half; frons commonly convergently aciculate; anterior half of pronotum declivous or not; elytral declivity usually convex, rarely impressed, granules absent or inconspicuous; mesocoxae rather widely separated by distance two or more times greater than width of pedicel; punctures on elytral disc almost always in rows (some exceptions); phloeophagus or spermophagous; introduced almost worldwide; apparently no endemic American species; broadleaf hosts and palm fruits; 1.3-3.7 mm . . . . ***Coccotryupes***

***Tiarophorus* Schreiner** [1882:246, Type-species: *Tiarophorus elongatus* Schreiner, monobasic. Synonyms: *Hypaspistes* Hagedorn 1908: 374, Type-species: *Hypaspistes camerunus* Hagedorn, monobasic, preoccupied; *Orthaspistes* Hagedorn 1909b: 733, Type-species: *Hypaspistes camerunus* Hagedorn, automatic; *Pseudothamnurgus* Eggers 1912a: 115, Type-species: *Thamnurgus scrutator* Pandellè, subsequent designation by Schedl 1961: 738]. Distribution: 13 species in Africa and S Europe.

***Dolurgocleptes* Schedl** [1965a: 61, Type-species: *Dolurgocleptes malgassicus* Schedl, monobasic]. Distribution: 1 species in Madagascar.

***Triotemnus* Wollaston** [1864: 264, Type-species: *Triotemnus subretusus* Wollaston, monobasic. Synonym: *Cladoctoproctus* Schedl 1975: 454, Type-species: *Cladoctoproctus scrafa* Schedl, original designation]. Distribution: 8 species in N Africa and the Canary Islands, 2 in India. Most species breed in the stems of *Euphorbia*, *Delphinium*, *Aconitum*, *Teucrium*, and *Bupierum*. Key: Peyerimhoff (1949).

***Thamnurgus* Eichhoff** [1864: 40, Type-species: *Bostrichus euphorbiae* Küster, subsequent designation by Hopkins 1914: 130]. Distribution: About 40 species in Asia, Europe, and Africa. A thorough review of the species of this and the next two genera would probably result in combining them into one genus. Keys: Reitter (1913: 85) for Europe, Balachowsky (1949: 165) for France.

***Taphronurgus* Reitter** [1913: 84, 90, Type-species: *Thamnurgus exul* Reitter, monobasic]. Distribution: 1 species in SE Europe to SW Asia. In *Clematis*. It is probable that this

genus will eventually be combined with *Thamnurgus*.

Xylocleptes **Ferrari** [1867: 37, Type-species: *Bostrichus bispinus* Duftschmidt, monobasic. Synonyms: *Xestips* Hagedorn 1912: 353, Type-species: *Xestips marginatus* Hagedorn, monobasic; *Hylonius* Nunberg 1973: 16, Type-species: *Hylonius brunneus* Nunberg, original designation]. Distribution: About 20 species in S Asia, S Europe, and Africa. Key: Reitter (1913: 91) for Europe.

Dendrocranulus **Schedl** [1937a: 165, Type-species: *Dendrocranulus tardus* Schedl, subsequent designation by Schedl 1938c: 169]. Distribution: 22 species in North and Central America, about 15 in South America and adjacent islands. Some species are monogamous, some are heterosanguineously polygynous; all bore in dying stems of Cucurbitaceae. Key: Wood (1982: 708) for North and Central America.

Dactylotrypes **Eggers** [1927a: 37, Type-species: *Dactylotrypes uyttenboogaarti* Eggers =*Xyloterus longicollis* Wollaston, monobasic]. Distribution: 1 species in the Canary Islands in fruits of *Phloenix canariensis* and *Dracaena drace*; it may have been introduced into France (Balachowsky 1949: 186). The male apparently joins the female in the parental gallery.

Lymantor **Lovendal** [1889: 25, 68, Type-species: *Lymantor sepicola* Lovendal =*Tomicus coryli* Perris, monobasic]. Distribution: 2 species in North America, 2 in Asia and Europe. All are heterosanguineously polygynous and xylophagous in small, dead branches of living trees. Keys: Reitter (1913: 91) for Europe, Wood (1982: 707) for North America.

Taphrorychus **Eichhoff** [1878a: 49, 204, Type-species: *Bostrichus bicolor* Herbst, subsequent designation by Hopkins 1914: 130. Synonyms: *Saliciphilus* Sokanovskii 1954: 17, 20, Type-species: *Hypothenemus machnovskii* Sokanovskii, original designation; *Pseudopoecilips* Murayama 1957: 614, Type-species: *Pseudopoecilips mikuniyamensis* Murayama, original designation; *Taphroterus* Schedl 1965b: 341, Type-species: *Taphroterus primitus* Schedl, monobasic]. Distribution: About 12 species in Asia, Europe, and N Africa. All are phloeophagous. Keys: Reitter (1913: 94), Balachowsky (1949: 193), Pfeffer (1962: 241).

Dendrographus **Schedl** [1964c: 310, Type-species: *Pelicerus pygmaeus* Eggers, original designation. Synonym: *Protopityophthorus* Schedl 1973: 73, Type-species: *Protopityophthorus durus* Schedl =*Pelicerus pygmaeus* Eggers, original designation]. Distribution: 1 species in New Guinea and New Britain Island.

Peridryocoetes **Wood** [1984: 230, Type-species: *Ozodendron nitens* Schedl, original designation, also cited but not described as a new genus by Schedl 1964a: 243]. Distribution: 3 species from Indonesia and New Guinea.

Cyrtogenius **Strohmeyer** [1910c: 127, Type-species: *Crytogenius bicolor* Strohmeyer, monobasic. *Cyrtogenius* Strohmeyer (1911: 16) a valid emendation of *Kyrtogenius*. Synonyms: *Carposinus* Hopkins 1915a: 9, 47, Type-species: *Carposinus pini* Hopkins, original designation: *Orosiotes* Niisima 1917: 1, Type-species: *Orosiotes kumatoensis* Niisima, monobasic; *Metahylastes* Eggers 1922: 165, Type-species: *Metahylastes africanus* Eggers, monobasic; *Pelicerus* Eggers 1923: 216, Type-species: *Lepicerus nitidus* Hagedorn, original designation; *Eulepiops* Schedl 1939b: 344, Type-species: *Eulepiops glaber* Schedl, original designation; *Ozodendron* Schedl 1957a: 13 and duplicate description by Schedl 1964a: 243, Type-species: *Pelicerus grandis* Beeson, monobasic; *Mimidendrulus* Schedl 1957a: 68, Type-species: *Mimidendrulus movoliae* Schedl, monobasic, the species designated by Schedl (1961: 732) was not an original species and is an invalid designation; *Carpophloeus* Schedl 1959b: 143, Type-species: *Carpophloeus rugipennis* Schedl, monobasic; *Taphroborus* Nunberg 1961: 617, Type-species: *Taphroborus vaticae* Nunberg, original designation; *Artepityophthorus* Schedl 1969: 157, Type-species: *Artepityophthorus aries* Schedl, monobasic; *Taphrostenoxis* Schedl, nomen nudum, for *Taphrostenoxis tenuis* Schedl, nomen nudum]. Distribution: About 16 species in Africa, more than 40 in the area from India and Japan to Australia and Micronesia. They are phloeophagous and heterosanguineously polygynous.

Dryocoetes **Eichhoff** [1864: 38, Type-species: *Bostrichus autographus* Ratzeburg, subsequent designation by Hopkins 1914:

121. Synonyms: *Anodius* Motschulsky 1860: 155, Type-species: *Bostrichus autographus* Ratzeburg, subsequent designation by Wood 1974: 232, suppressed by International Commission on Zoological Nomenclature 1979: 149; *Dryocoetinus* Balachowsky 1949: 180, Type-species: *Bostrichus villosus* Fabricius, original designation]. Distribution: 7 species in North America, about 80 in Asia, Europe, and Africa have been assigned to this genus, but more than half of them have been transferred to other genera. All are heterosanguineously polygynous and phloeophagous. Keys: Reitter (1913: 75) for Europe, Murayama (1957: 594) for Japan and vicinity, Bright (1963: 107) and Wood (1982: 724) for North America.

***Chiloxylon* Schedl** [1959c: 550, Type-species: *Chiloxylon rufulus* Schedl, monobasic]. Further study of this genus is needed; it may be allied to *Dendroterus* of the Corthylini (Pityophthorina), rather than to *Dryocoetes*. Distribution: 1 species in Brazil (Matto Grosso).

***Dryocoetiops* Schedl** [1957a: 13, Type-species: *Ozopemon laevis* Strohmeyer, original designation]. Distribution: About 15 species in SE Asia, Sri Lanka (Ceylon), Indonesia, and New Guinea. One species observed in nature appeared to be consanguineously polygynous (or some form of parthogenesis) and was myelophagous.

***Ozopemon* Hagedorn** [1908: 382, Type-species: *Ozopemon regius* Hagedorn, monobasic]. Distribution: About 27 species in SE Asia and Indonesia to Fiji. All are consanguineously polygynous and phloeophagous.

***Coccotrypes* Eichhoff** [1878a: 308, Type-species: *Bostrichus dactyliperda* Fabricius, subsequent designation by Hopkins 1914: 118. Synonyms: *Poecilips* Schaufuss 1897: 110, Type-species: *Poecilips sannio* Schaufuss, monobasic; *Cryphaloides* Formenek 1908: 91, Type-species: *Cryphaloides donisthorpei* Formenek =*Bostrichus carpophagus* Hornung, monobasic; *Thamnurgides* Hopkins 1915a: 45, Type-species: *Thamnurgides persicae* Hopkins =*Coccotrypes advena* Blandford, original designation; *Spermatoplex* Hopkins 1915a: 48, Type-species: *Spermatoplex rhizophorae* Hopkins, original designation; *Dendrurgus* Eggers 1923: 144, Type-species: *Dendrurgus rhizophorae* Eggers =*Spermatoplex rhizophorae* Hopkins, subsequent designation by Wood 1982: 731; *Hyphaene* Hagedorn 1913: 254, nomen nudum, Type-species: *Hyphaene guineensis* Hagedorn, nomen nudum =*Bostrichus carpophagus* Hornung, no status]. Distribution: More than 100 species have been assigned to this genus, mostly from Africa, S Asia, and adjacent areas. Species in most other areas have been introduced through commerce. All are consanguineously polygynous and phloeophagous or spermophagous; a few species may assume both feeding habits. This exceedingly difficult genus is in a state of taxonomic chaos. Key: Wood (1982: 732) for North America.

Tribe Crypturgini

Crypturgi LeConte [1876: 374, 387, Type-genus: *Crypturgus* Erichson, 1836]

DESCRIPTION.—Frons usually not dimorphic, male sometimes slightly impressed, female convex; eye deeply emarginate, except sinuate in *Deropria*; antennal scape moderately long, slender, funicle 2- to 3-segmented, club comparatively small, two sutures on apical half, 1 sometimes septate, both frequently absent; pronotum usually unarmed; procoxae contiguous; protibia flattened, lateral margin armed by several socketed denticles; scutellum visible; elytral punctures in rows or confused, setae hairlike; anterior surfaces and (frequently) elytra uniformly reticulate.

BIOLOGY.—They are monogamous and phloeophagous except that those species associated with *Euphorbia* bore throughout subepidermal tissues of recently killed stems, apparently with little regard to the cambium. *Crypturgus* usually utilizes the entrance tunnel of another insect. Larval mines are independent. Details of the habits have not been studied.

TAXONOMY.—This tribe apparently was derived from the same ancestral stock that gave rise to the Dryocoetini, although the true affinities have not been worked out. It appears to have arisen well into the Tertiary in the Ethiopian realm where at least some members of five of the six known genera occur today. *Crypturgus* appears to have reached North America from Asia rather recently. *Dolurgus* (North America) appears to be a primitive relict of an earlier radiation that is now extinct except for this species.

Key to the Genera of Crypturgini

1. Antennal funicle 3-segmented, club with sutures 1 and 2 recurved, clearly marked by grooves and rows of setae, 1 almost at middle of club; pronotum longer than wide, unarmed, a distinct constriction on anterior third; elytra rather coarsely striate, strial setae largely obsolete, interstrial setae short; W North America; *Abies, Picea, Pinus*; 1.6-1.9 mm ...... ***Dolurgus***

— Antennal funicle 2-segmented, club with no more than 1 suture indicated or if 2 present then club constricted at septate suture 1 2

2(1). Antennal club rather strongly constricted at middle at suture 1; elytral punctures confused or striae, if indicated, not impressed, strial punctures little larger than those of interstriae 3

— Antennal club not constricted at middle, suture 1 obsolete or indicated only by a partial, internal septum 4

3(2). Elytral declivity strongly flattened to concavely impressed; pronotum wider than long, weakly if at all declivous on anterior half, never armed by granules, anterior margin unarmed; N Africa; *Euphorbia*; 1.6-2.6 mm .... ***Coleobothrus***

— Elytral declivity convex; pronotum usually longer than wide, anterior half more strongly declivous, often armed by granules, anterior margin elevated as a costa, serrate, or dentate; Canary Islands, Africa to India; *Euphorbia*; 1.3-2.3 mm .... ***Aphanarthrum***

4(2). Antennal club unmarked by sutures; anterior half of pronotum declivous and armed by coarse asperities, anterior margin serrate; eye entire to feebly sinuate; Canary Islands; host unknown; 1.5-2.0 mm .... ***Deropria***

— Antennal club with suture 2 marked at apex, if present, suture 1 sometimes indicated by an internal septum; pronotum weakly declivous, unarmed, anterior margin never serrate; eye deeply emarginate 5

5(4). Remnants of sutures 1 and 2 usually present in antennal club; elytral striae more strongly impressed, punctures rather coarse, always in rows; elytral vestiture on disc short, longest setae shorter than distance between interstrial rows; North America, Asia, Europe, N Africa; Pinaceae; 0.9-1.5 mm .... ***Crypturgus***

— Antennal club usually without indications of sutures; elytral striae usually not impressed, punctures much smaller and usually confused; discal vestiture longer, longest setae distinctly longer than distance between interstrial rows; Canary Islands, S Europe, N Africa; *Euphorbia*; 1.1-1.7 mm .... ***Cisurgus***

Dolurgus **Eichhoff** [1868a: 147, Type-species: *Hylastes pumilus* Mannerheim, monobasic]. Distribution: 1 species in W North America (Alaska to N California). It is monogamous and phloeophagous.

Coleobothrus **Enderlein** [1929: 144, Type-species: *Coleobothrus jandiacus* Enderlein, original designation]. Distribution: 2 species in the Canary Islands and 2 in Africa. Key: Menier (1973: 208).

Aphanarthrum **Wollaston** [1854: 292, Type-species: *Aphanarthrum euphorbiae* Wollaston, monobasic]. Distribution: About 30 species in the Canary Islands, Africa, and India. Key: Schedl (1959a: 56).

Deropria Enderlein [1929: 143, Type-species: *Aphanarthrum elongatum* Eggers, original designation]. Distribution: 1 species in the Canary Islands.

Crypturgus **Erichson** [1836: 60, Type-species: *Bostrichus pusillus* Gyllenhal, designated by Thomson 1859: 147]. Distribution: 3 species in North America, 10 in Asia, Europe, N Africa, and adjacent islands. All are monogamous and phloeophagous. Keys: Reitter (1913: 61) for Europe, Swaine (1918: 54) and Wood (1982: 740) for North America, Schedl (1946: 4) for Europe and Asia, Bright (1976: 114) for Canada.

Cisurgus **Reitter** [1894: 59, 65, Type-species: *Cisurgus filum* Reitter, monobasic]. Distribution: 6 species in SW Asia, S Europe, N Africa, and the Canary Islands. Key: Schedl (1959: 28).

Tribe Xyloterini

Xyloteroideae Lindemann [1876: 165, Type-genus: *Xyloterus* Erichson, 1836 =*Trypodendron* Stephens, 1830]

Trypodendron Trèdl [1907: 18, Type-species: *Trypodendron* Stephens, 1830]

DESCRIPTION.—Frons dimorphic, male weakly to very strongly impressed, female convex; eye completely divided; antennal scape long, funicle 4-segmented (Fig. 51), club without sutures, basal area sometimes corneous, derived from obliquely truncate type; procoxae contiguous, proepimeron of female with mycetangium; pronotum asperate on anterior slope; protibia flat in male, inflated and armed by small unsocketed denticles on posterior face in female; scutellum visible; elytra conservatively sculptured.

BIOLOGY.—All species are monogamous and xylomycetophagous. The male joins the female in parental galleries. The eggs are deposited in niches above and below in the egg tunnels. The larvae enlarge the niches into

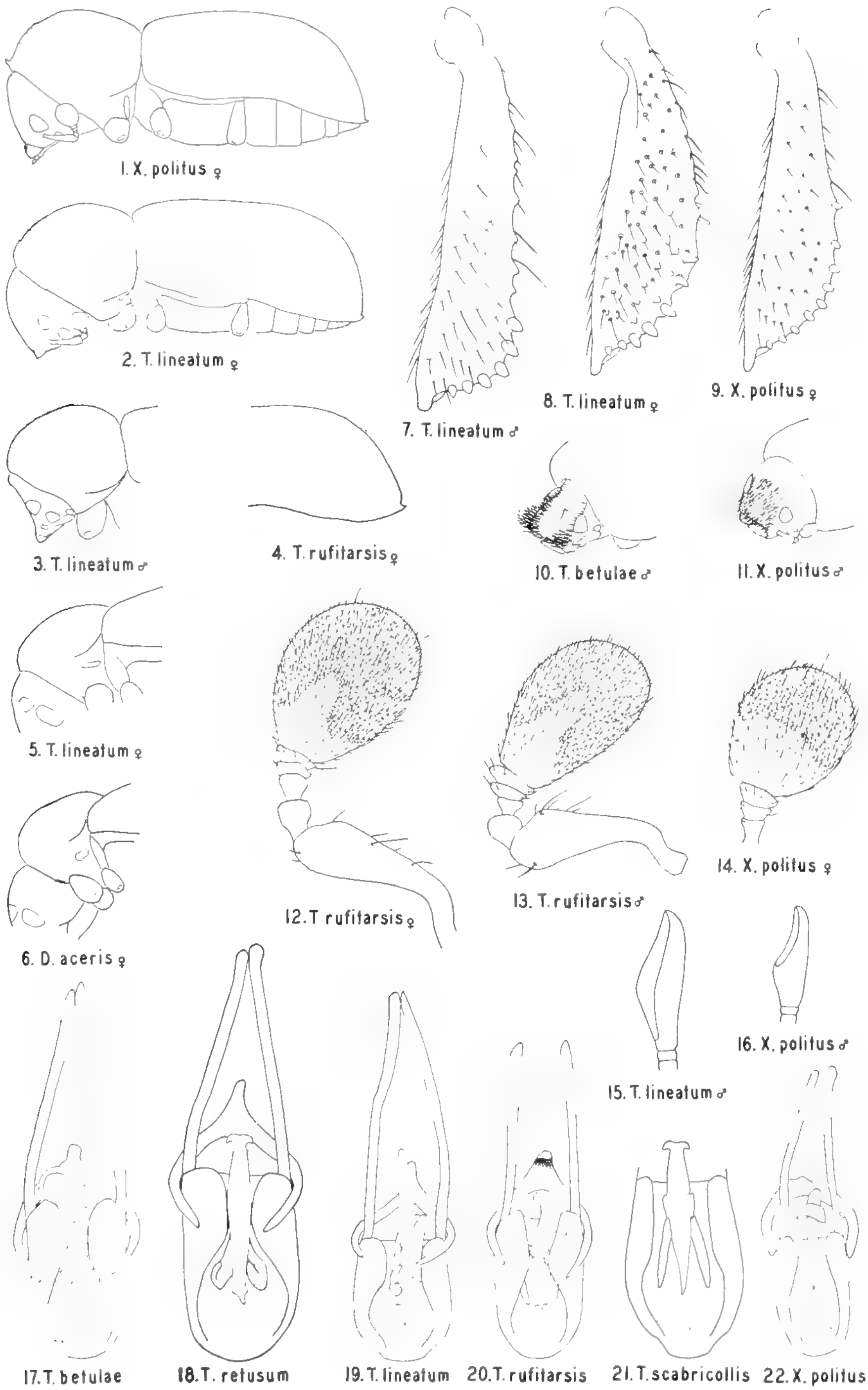


Fig. 51. Xyloterini spp.: 1, *Xyloterinus politus* (Say), outline of female; 2 and 5, *Trypodendron lineatum* (Olivier), female; 3, *T. lineatum*, male; 6, *Indocryphalus aceris* (Niisima), female; 7, *T. lineatum*, male; 8, *T. lineatum*, female; 9, *X. politus*, female protibia; 10, *T. betulae* Swaine, male head; 11, *X. politus*, male head; 12, *T. rufitarsis* (Kirby), female; 13, *T. rufitarsis*, male; 14, *X. politus*, female antenna; 15, *T. lineatum* female antenna; 16, *X. politus*, male antenna; 17-22, male genital capsul, dorsal aspect, as labeled.

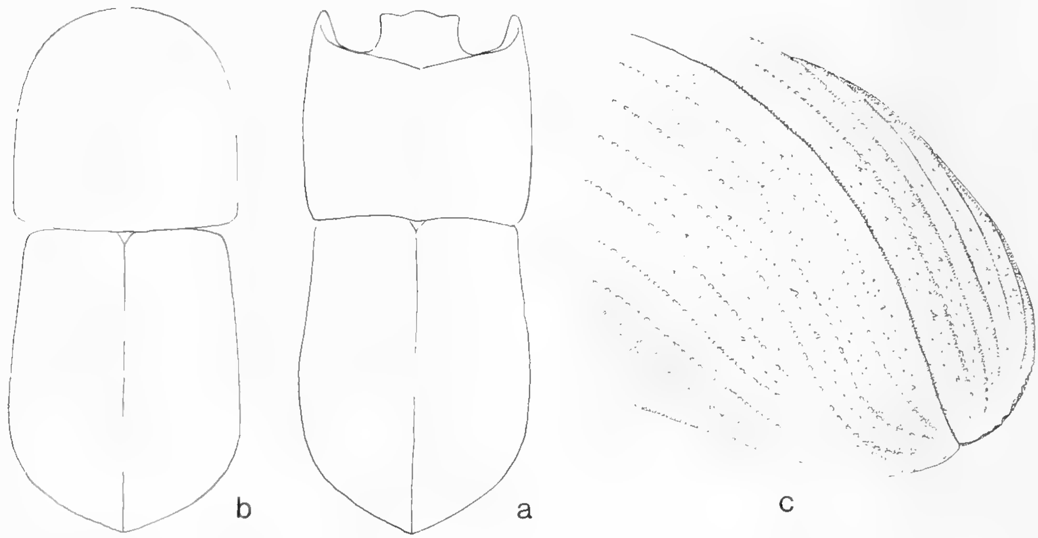


Fig. 52. *Xyleborus spathipennis* Eichhoff: A, outline of male, dorsal aspect; B, dorsal aspect of female; C, female declivity (setae omitted).

cradles just enough to accommodate the newly transformed adult beetle. The brood emerges through the parent entrance tunnel. Temperate species overwinter in litter on the forest floor.

TAXONOMY.—This is a small group consisting of three small genera. They appear to have been derived from the same parental stock that gave rise to the Xyleborini. They apparently originated in Asia, with *Trypodendron* extending westward into Europe and eastward in late Tertiary to northern North America. *Xyloterinus* (North America) and *Indocryphalus* (Asia) were derived from the same parental stock, with *Xyloterinus* apparently reaching North America in the warm period that preceded the last ice age.

Key to the Genera of Xyloterini
(Modified from Wood 1957b: 344)

1. Basal area of antennal club distinctly subcorneous, its apical margin strongly, rather narrowly procurved on anterior face; protibia thickened, posterior face tuberculate in female, flattened and usually finely tuberculate in male; male frons broadly, deeply excavated from epistoma to vertex, convex in female; male pronotum subquadrate, anterior margin straight to slightly recurved and unarmed, female anterior margin procurved and armed by several teeth; long axis of proepimeral excavation of female longitudinal and very narrow; North America, N Asia, Europe; coniferous and broadleaf trees; 2.7-4.6 mm .... ***Trypodendron***

— Basal area of antennal club broadly, weakly procurved or else not at all corneous; protibia flattened and unarmed on posterior face in both sexes; anterior margin of pronotum procurved and armed by a series of teeth in both sexes 2

2(1). Basal area of antennal club not thickened or corneous, uniformly pubescent to base; males and females equal in size; anterior margin of pronotum slightly produced at median line in male; long axis of proepimeral excavation of female longitudinal, short to long, narrow to rather broad; SE Asia; broadleaf hosts; 2.6-3.5 mm .... ***Indocryphalus***

— Basal area of antennal club subcorneous, thickened, weakly procurved on anterior face; male distinctly smaller than female; anterior margin of male pronotum as in female except some teeth reduced or absent; proepimeral excavation of female transverse, rather large, broad; North America; broadleaf hosts; 2.7-3.7 mm . ***Xyloterinus***

Trypodendron **Stephens** [1830: 353, Type-species: *Dermestes domesticus* Linnaeus, subsequent designation by Westwood 1838: 39 and Thomson 1859: 146. Synonym: *Xyloterus* Erichson 1836: 60, Type-species: *Bostrichus lineatus* Olivier, subsequent designation by Thomson 1859: 146]. Distribution: 5 species in North America, about 9 in Asia and Europe. All are monogamous and xylomycetophagous. Keys: Schedl (1951c: 86) for Europe and Asia, Wood (1957b: 345, 1982: 747) for North America.

Indocryphalus **Eggers** [1939: 5, Type-species: *Indocryphalus malaisei* Eggers =*Xy-*

loterus intermedius Sampson, original designation. Synonym: *Dendrotrypum* Schedl 1951c: 76, Type-species: *Xyloterus aceris* Niisima, subsequent designation by Browne 1970: 76, Type-species: *Xyloterus aceris* Niisima, subsequent designation by Browne 1970: 562]. Distribution: About 9 species in Asia (India to Japan). Apparently all are monogamous and xylomycetophagous. Key: Schedl (1951c: 77). Catalog: Browne 1970: 562).

***Xyloterinus* Swaine** [1918: 44, 83, Type-species: *Bostrichus politus* Say, original designation]. Distribution: 1 species in E North America. It is monogamous and xylomycetophagous.

Tribe Xyleborini

Xylebori LeConte [1876: 346, 358, Type-genus: *Xyleborus* Eichhoff, 1864]

Webbinae Hopkins [1915b: 224, Type-genus: *Webbia* Hopkins. 1915]

DESCRIPTION.—Body dimorphic, male dwarfed, deformed, flightless, eye reduced in size, often aberrant in shape (Fig. 52); frons convex, unadorned; eye emarginate to divided in a few oriental forms; antennal scape elongate, funicle 5-segmented except 3- or 4-segmented in a few oriental forms, club obliquely truncate except basal corneous area reduced or absent in some genera; pronotum asperate on anterior slope (a few exceptions, especially in male), procoxae varying from contiguous to widely separated; scutellum varying from large and flat to modified to absent; elytra variable, conservatively to elaborately sculptured; meso- and metatibiae flat, broad, tapered on distal third, lateral margin armed by a row of numerous, small, closely set socketed teeth, these usually alternating with marginal or submarginal setae in more highly evolved forms; meso- and metatarsi retractible into tibial grooves.

BIOLOGY.—Consanguineous polygyny is universal, apparently all males are haploid, deformed, and flightless. All are xylomycetophagous. Eggs are deposited in clusters in the parental tunnels. The larvae usually extend the parental galleries or feed exclusively on the fungal mycelium in the parental tunnels. The brood emerges through the parental entrance tunnel. Temporate species may overwinter either in the brood host or in litter on the forest floor. At least one species (*Xyleborus dispar*) passes through a definite dipause in the adult stage during the winter months.

TAXONOMY.—The worldwide circumtropical distribution of this tribe, with a few species occurring in temperate areas, suggests that it is at least moderately old. The occurrence of the same species groups of *Ambrosiodmus* in Africa and South America indicates that the basic characters of groups within that genus had been fixed by early Tertiary. However, the distributions of other groups and the large number of species in the tribe indicate that very rapid, recent evolution is in progress. In this tribe, arrhenotocous parthenogenesis is universal. This suggests a possible relationship to the higher Dryocoetini; however, a relationship to the Xyloterini is more likely. Because of the recent, active evolution affecting this group, generic limits are not clearly defined. Common and particularly confusing features of this tribe are size races within what otherwise appears to be a single species; in some cases these behave as entirely different species and in others, involving those same forms, there is total intergradation of the two sizes. This is probably a product of this type of mating system that will be more fully understood when details of their habits are known.

The generic classification of this tribe presented below is tentative and flawed; however, it is presented as a first attempt to organize a very large and difficult group even though a third of the species in the tribe were not studied. It is hoped that it might give at least limited direction to those who will concentrate more particularly on this group.

Key to the Genera of Xyleborini
(Females only)

1. Basal segment of labial palpus cylindrical, only slightly wider than segment 2 or 3, none of segments ornamented by a special tuft of setae; pregula and adjacent surfaces flush with general contour of ventral surface of head; antennal club rather strongly flattened, without visible sutures, corneous area reduced, usually pubescent to base; lateral margins of pronotum acutely elevated, pleural area concave (on transverse axis); anterior margin of pronotum unarmed; protibia inflated, armed on its posterior face by minute tubrercles; Africa; 2 species introduced into America; 1.4-4.7 mm .... ***Premnobius***

— Basal segment of labial palpus enlarged, conspicuously wider than segment 2 or 3; its posterior face usually flat, one or more segments ornamented by specialized setae; pregula and adjacent areas usually conspicuously impressed below general contour of head 2

2(1). Antennal club with sutures 1 and 2 rather strongly procurved, both segments 1 and 2 corneous and mostly glabrous except at sutures; protibia slender, almost cylindrical, posterior face armed by tubercles; lateral margins of pronotum acutely elevated, pleural area transversely concave; body very slender; anterior margin of pronotum armed by 2 or more very coarse serrations; domicile parasites of other ambrosia beetles; Mexico to Brazil; 2.7-6.0 mm . . . . ***Sampsonius***

— Antennal club obliquely truncate or nearly so, sutures (when visible) on or very near margin of corneous area, recurved (except pubescent to base in some oriental forms); protibia usually more strongly expanded on apical half; lateral margins of pronotum rounded (except *Cnestus*, *Webbia*); "parasitic" habit unknown 3

3(2). Scutellum visible, moderately large, its surface flush with adjacent surface of elytra; ventral margin of metafemur either rounded or rather obtusely angulate, on its posterior face groove for reception of tibia usually clearly indicated on distal half 4

— Scutellum either not visible or (*Xyleborinus*) base of elytra at suture notched thereby exposing cone-shaped scutellum that appears displaced cephalad, or (couplet 20) scutellum visible on anterior face of declivital slope of elytral bases; scutellar area usually with abundant setae associated with mycetangium; metafemur usually more strongly flattened, its (longitudinal) ventral margin attenuately, very acutely angulate (except *Schedlia*), groove for reception of tibia visible only near apical joint 16

4(3). Posterior face of antennal club marked by 2 sutures on apical third (suture 2 poorly represented in some *Coptoborus*), anterior face with apical portion convex (or concave only distad from segment 2), segment 2 comparatively large, sclerotized, protibia armed by 6 or 7 socketed teeth on lateral margin, metatibia with 6 to 9 socketed teeth; anterior coxae always contiguous 5

— Posterior face of antennal club with no more than 1 suture visible at or very near apex (usually none), apical portion of anterior face usually flat to concave, segment 2 (if visible) not corneous; number of metatibial teeth variable; anterior coxae contiguous or separated . 8

5(4). Protibia with posterior face inflated and armed by numerous fine tubercles; metatibia usually with 8 or 9 socketed teeth; segment 2 on antennal club usually forming a complete, oblique annulus, on anterior face its apical margin usually acutely costate as on segment 1; Mexico to South America (1 species introduced into Africa); 2.1-5.3 mm . . ***Dryocoetoides***

— Protibia with posterior face flat, unarmed, metatibia almost never with more than 7 socketed teeth 6

6(5). Declivity commencing at or anterior to middle of elytra, its lower half transversely, broadly impressed and either flat or shallowly concave; if discal interstrial punctures uniseriate then declivital surface covered by dense, confused, small scales, if declivital setae hairlike then discal interstrial punctures rather dense, confused; India to Philippines and New Guinea; 2.2-5.0 mm . . . . . ***Leptoxyleborus***

— Elytral declivity usually convex, commencing either posterior to middle or strongly tapered on posterior half, never with a strong transverse impression; elytra never ornamented by scales 7

7(6). Posterior fourth of elytra comparatively broad, rather broadly rounded behind, suture never emarginate; declivital interstriae 1 to 3 similar, tubercles minute, if present; body comparatively stout, less than 2.6 times as long as wide; Mexico to South America; introduced to Africa; 1.7-3.0 mm . . . . ***Theoborus***

— Posterior third of elytra attenuate or acuminate, narrowly rounded behind, suture often emarginate; 1 or more declivital interstriae sometimes armed by small denticles; body slender, at least 2.6 times as long as wide; Mexico and South America, Africa to SE Asia; 1.5-5.0 mm . . . . ***Coptoborus***

8(4). Protibia with posterior face inflated and armed by numerous fine tubercles; posterior face of antennal club either with or without a suture; elytral declivity and at least part of disc with interstriae carinate (carinae sometimes reduced to rows of tubercles), strial spaces between carinae usually granular or dull, with punctures usually obsolete; SE Asia to Australia; 1.3-3.1 mm . . . . ***Arixyleborus***

— Protibia with posterior face almost flat, smooth; elytra with different sculpturing 9

9(8). Antennal club with segment 2 on anterior face usually conspicuous, sometimes rather large, apical margin of segment 1 on both faces rounded, often inconspicuous or absent on anterior face, almost always visible on subapical area of posterior face; procoxae always contiguous, intercoxal piece longitudinally emarginate, posterior element of intercoxal piece never inflated or armed, mesocoxae usually more widely separated by distance greater than thickness of scape 10

— Segment 1 of antennal club corneous, its distal margin very acutely elevated into a continuous costa (forming a complete circle) extending from anterior face to apex, suture almost never visible on posterior face; procoxae varying from contiguous to widely separated, if

contiguous then posterior intercoxal piece sometimes inflated and armed; mesocoxae usually subcontiguous, usually separated by distance less than thickness of scape 13

10(9). Pronotal asperities extending to base, including most of discal area (except numerous African, etc. species without discal asperities); anterior margin of pronotum never armed by a definite row of serrations; lateral margin of porotibia armed by 7 to 8 socketed denticles, metatibia by 8 to 11 denticles; pantropical; 1.9-4.2 mm ..... ***Ambrosiodmus***

— Pronotal asperities confined to slightly more than anterior half; lateral margin of metatibia armed by more than 11 socketed denticles .. 11

11(10). Elytra obliquely, abruptly truncate, usually with an acutely, distinctly elevated circumdeclivital, subcircular costa, face of declivity flat to concave (when costa incomplete then antennal club pubescent to base); discal interstriae with punctures uniseriate, occasionally slightly confused on some interstriae (strongly confused in superficially similar *mancus* group of *Xylosandrus*); antennal club usually pubescent to its base, more strongly flattened; eye deeply emarginate to entirely divided; SE Asia to Australia; 2.4-3.1 mm . ***Amasa***

— Declivital margin rounded, a carina not indicated on its basal two-thirds, declivital face basically convex; antennal club obliquely truncate (except pubescent to base in a few *Xyleborus* 12

2(11). Pronotum commonly subquadrate, its anterior margin almost always unarmed, posterolateral margin of declivity subacutely elevated from sutural apex to interstriae 7; strial and interstrial punctures usually in rows, elytral vestiture comparatively sparse, confined to strial and interstrial rows; Asia and Australia to Africa; 2.4-4.6 mm .. ***Euwallacea***

— Pronotum almost never quadrate, its anterior margin usually procurved and armed by a definite row of serrations; posterolateral margin of declivity rounded; elytral punctures often confused, vestiture usually much more abundant; SE Asia to Africa; 2.1-4.1 mm ... ***Terminalinus***

13(9). Procoxae contiguous, intercoxal piece longitudinally emarginate (a few individuals in *javanus* group subcontiguous but only feebly emarginate), its posterior element inflated, occasionally dentate; body usually more slender, mostly more than 2.0 times as long as wide; tropical and temporate areas worldwide; 1.7-5.9 mm .... ***Xyleborus***

— Either funicle 4-segmented or if 5-segmented then procoxae moderately to rather widely separated, intercoxal piece continuous, not longitudinally emarginate (a slight notch in a few *Taurodemus*); body usually stouter, mostly less than 1.9 times as long as wide ... 14

14(13) Lateral margin of protibia armed by 9 to 12 socketed teeth; elytral declivity moderately to very strongly sulcate on at least basal half, lateral margins armed by at least 1 major spine and several smaller tubercles; antennal funicle 5-segmented; Central and South America; 2.4-4.5 mm .... ***Taurodemus***

— Lateral margin of protibia armed by 4 to 7 socketed teeth; elytral declivity usually not conspicuously sulcate, lateral margins not conspicuously armed by spines or tubercles . 15

15(14). Lateral margins of pronotum rounded (subacute in *morigerus*); funicle 5-segmented; corneous area (in central portion) occupying basal third of antennal club; eye about one-third divided by an emargination; protibia armed on lateral margin by 4 to 6 socketed teeth; pantropical; 1.3-5.0 mm .... ***Xylosandrus***

— Lateral margins (and usually basal margin) of pronotum subacutely elevated, costate; antennal funicle 4-segmented (some 5-segmented?); corneous area (in central portion) occupying less than basal fourth of antennal club; eye feebly if at all emarginate; protibia armed on lateral margin by 6 to 8 socketed teeth; SE Asia to Australia; 2.0-4.0 mm .... ***Cnestus***

16(3). Basal margins of elytra distinctly, shallowly emarginate in scutellar area, emargination usually filled by dense setae, scutellum displaced slightly cephalad into a visible, conical process; posterior face of antennal club without sutures; protibia flat, its lateral margin armed by 6 to 8 socketed denticles, all on apical half; strial punctures in rows; declivity usually armed by tubercles or spines; tropical and temporate areas worldwide; 1.4-3.5 mm ... ***Xyleborinus***

— Basal margins of elytra not emarginate at suture, scutellum not conical, with other combinations of characters 17

17(16). Antennal funicle 5-segmented; lateral margin of protibia armed by socketed denticles on less than apical half 18

— Antennal funicle 3- or 4-segmented; protibia inflated but not asperate on posterior face, its lateral margin armed (usually to base) by socketed teeth on more than apical three-fourths 23

18(17). Pronotum asperate to base, including discal area; basal corneous area occupying almost three-fourths length of club, its apical margin straight, not acutely elevated, suture 2 clearly indicated (club more reminiscent of *Hylastes* than of *Xyleborus*), suture 1 visible near apex on posterior face; scutellum visible on anterior slope of elytral base; punctures on elytral disc confused on basal third, in obscure rows behind; strial and interstrial hair moderately long; all tibiae very broad; New Zealand; 1.9 mm . ***Mesoscolytus***

— Discal area of pronotum unarmed by asperities, smooth; basal corneous area of antennal club occupying less than basal half in central area, its apical margin recurved 19

19(18). Posterior face of antennal club unmarked by sutures, acute costa marking apical margin of corneous area usually forming a complete ring; scutellum usually visible on anterior declivous slope of elytral margins; body stout (less than 1.8 times as long as wide), usually black in color; punctures on elytral disc dense, confused 20

— Posterior face of antennal club with at least 1 suture visible, apical margin of corneous area never costate; scutellum not visible on anterior slope at bases of elytra; body more slender (at least 2.0 times as long as wide), color usually yellowish to reddish brown 21

20(19). Metatibia normal, socketed denticles present on lateral margins; metatarsus normal, neither unusually long nor abnormally compressed; declivity mostly restricted to posterior half of elytra, convex or moderately impressed, unarmed; India to Philippines and Australia; 4.0-6.0 mm . . . . ***Hadrodemius***

— Metatibia abnormally large and broad, socketed denticles on lateral margin obsolete; metatarsus unusually long, very strongly compressed; declivity extending almost to base of elytra, armed by very coarse spines; Philippines and New Guinea to Africa; 1.1-4.0 mm . . . . ***Eccoptopterus***

21(19). Protibia inflated and densely asperate on posterior surface; anterior face of mesotibia similarly but less strongly inflated and armed; elytral disc smooth and shining, abruptly becoming rugose-reticulate on declivity, discal punctures confused, declivity variously armed by rather large spines; Sumatra to New Guinea; 4.0-5.0 mm . . . . ***Schedlia***

— Pro- and mesotibiae neither inflated nor armed on posterior face; declivity never densely, uniformly rugose-reticulate, if armed then spines small; size much smaller . 22

22(21). Strial punctures in definite rows (except confused in *bellus* group); declivity convex, without a marginal costa, variously sculptured; elytral scales never present; SE Asia and Indonesia to Philippines; 1.4-3.4 mm . . . . ***Coptodryas***

— Elytral punctures small, confused; declivity commencing on basal half of elytra, very strongly concave, its marginal crest forming a blunt, elongate, circumdeclivital costa, inner face ornamented by abundant, small scales or long hair; Indonesia; 3.3-3.5 mm . . . . ***Taphrodasus***

23(17). Elytra moderately acuminate on declivity and mucronate at sutural apex; base of declivity rounded, unarmed; base of elytra often with a submarginal mycetangium; Malaya; 2.2 mm . . . . ***Cryptoxyleborus***

— Elytra variously convex or truncate at base of declivity, never acuminate or mucronate at sutural apex; declivital margin abrupt, usually armed; SE Asia to New Guinea and Philippines; 1.5-3.0 mm . . . . ***Webbia***

Premnobius **Eichhoff** [1878a: 65, 404, Type-species: *Premnobius cavipennis* Eichhoff, monobasic. Synonym: *Premnophilus* Browne 1962a: 79, Type-species: *Xyleborus joveri* Schedl, original designation]. Distribution: 24 species in Africa, 2 of them were introduced into America. All are consanguineously polygynous and xylomycetophagous. Key: Wood (1982: 756).

Sampsonius **Eggers** [1933a: 23, nomen nudum, 1935: 157, Type-species: *Sampsonius sexdentatus* Eggers, original designation]. Distribution: 4 species in S Mexico and Central America, about 7 species in South America. All are domicile parasites of other ambrosia beetles and are consanguineously polygynous and xylomycetophagous. Key: Wood (1982: 759) for Central America.

Dryocoetoides **Hopkins** [1915a: 10, 52, Type-species: *Dryocoetoides guatemalensis* Hopkins =*Xyleborus capucinus* Eichhoff, original designation]. Distribution: 2 species in Central America, about 22 in South America 1 of which was introduced into Africa. All are consanguineously polygynous and xylomycetophagous. Key: Wood (1982: 762) for Central America.

Leptoxyleborus **Wood** [1980: 94, Type-species: *Phloeotrogus sordicauda* Motschulsky, original designation]. Distribution: 4 species in SE Asia. All are consanguineously polygynous and xylomycetophagous.

Theoborus **Hopkins** [1915a: 57, Type-species: *Theoborus theobromae* Hopkins, original designation]. Distribution: 9 species in Central America, several additional species in South America belong here. All are consanguineously polygynous and xylomycetophagous. Key: Wood (1982: 770) for Central America.

Coptoborus **Hopkins** [1915a: 10, 53, Type-species: *Coptoborus emarginatus* Hopkins =*Xyleborus vespatorius* Schedl, original designation. Synonym: *Streptocranus* Schedl 1939a: 52, Type-species: *Streptocranus mirabilis* Schedl, monobasic]. Distribution: 5 species in Central America, about 10 in South America, and about 6 in SE Asia and adjacent islands. All are consanguineously polygynous

and xylomycetophagous. Key: Wood (1982: 780) for Central America.

***Arixyleborus* Hopkins** [1915a: 10, 59, Type-species: *Arixyleborus rugosipes* Hopkins, original designation. Synonym: *Xyleboricus* Eggers 1923: 212, Type-species: *Xyleboricus canaliculatus* Eggers, subsequent designation by Schedl 1936b: 64]. Distribution: About 42 species in SE Asia to Australia and the Philippines. All are consanguineously polygynous and xylomycetophagous.

***Ambrosiodmus* Hopkins** [1915a: 10, 55, Type-species: *Xyleborus tachygraphus* Zimmermann, original designation. Synonyms: *Phloeotrogus* Motschulsky 1863: 127, Type-species: *Phloeotrogus obliquecaudata* Motschulsky, designated by Hopkins 1914: 127, International Commission on Zoological Nomenclature 1979: 151, name rejected; *Browneia* Nunberg 1963: 37, Type-species: *Xyleborus illepidus* Schedl =*Pityophthorus obliquus* LeConte, original designation]. Distribution: 11 species in North and Central America, about a dozen in South America, numerous species (40 or more) in Asia and Africa. All are consanguineously polygynous and xylomycetophagous. Key: Wood (1982: 781) for North and Central America.

***Amasa* Lea** [1894: 322, Type-species: *Amasa thoracicus* Lea, monobasic. Synonyms: *Pseudoxyleborus* Eggers 1930: 206, Type-species: *Pseudoxyleborus beesoni* Eggers, monobasic; *Anaxyleborus* Wood 1980: 90, Type-species: *Tomicus truncatus* Erichson, original designation]. Distribution: About 35 species in India and Malaya to Australia. All are consanguineously polygynous and xylomycetophagous.

***Euwallacea* Hopkins** [1915a: 10, 54, Type-species: *Xyleborus wallacei* Blandford, original designation]. Distribution: About 50 or more species in Africa to SE Asia and Australia. All are consanguineously polygynous and xylomycetophagous.

***Terminalinus* Hopkins** [1915a: 10, 57, Type-species: *Terminalinus terminaliae* Hopkins, original designation. Synonyms: *Kelantanius* Nunberg 1961: 621, Type-species: *Xyleborus punctatopilosus* Schedl, original designation]. Distribution: About 30 or more species in Africa to SE Asia and Australia. All are consanguineously polygynous and xylomycetophagous.

***Xyleborus* Eichhoff** [1864: 37, Type-species: *Bostrichus monographus* Fabricius, subsequent designation by Lacordaire 1866: 381. Synonyms: *Anisandrus* Ferrari 1867: 24, Type-species: *Xyleborus (Apate) dispar* Fabricius, monobasic; *Anaeretus* Dugès 1887: 141, Type-species: *Xyleborus guanajuatensis* Dugès =*Bostrichus volvulus* Fabricius, monobasic, neotype for type-species designated by Wood 1983: 650; *Progenius* Blandford 1896a: 20, Type-species: *Progenius fleutiauxi* Blandford =*Xyleborus subcostatus* Eichhoff, subsequent designation by Hopkins 1914: 128; *Cyclorhipidion* Hagedorn 1912: 355, Type-species: *Cyclorhipidion pelliculosum* Hagedorn =*Xyleborus prelaetus* Schedl, monobasic; *Heteroborips* Reitter 1913: 79, 82, Type-species: *Bostrichus cryptographus* Ratzeburg, monobasic; *Xyleborips* Reitter 1913: 79, 111, Type-species: *Xyleborus meuseli* Reitter, monobasic; *Boroxylon* Hopkins 1915a: 10, 58, Type-species: *Boroxylon stephegynis* Hopkins =*Phloeotrogus bidentatus* Motschulsky, original designation; *Notoxyleborus* Schedl 1934: 84, Type-species: *Notoxyleborus kalshoveni* Schedl, monobasic]. Distribution: Several hundred species almost worldwide. All are consanguineously polygynous and xylomycetophagous. Keys: Bright (1968: 1296, 1976: 131) for North America, Wood (1982: 778) for North and Central America, Reitter (1913: 81) for Europe.

***Taurodemus* Wood** [1980: 96, Type-species: *Xyleborus sharpi* Blandford, original designation]. Distribution: 14 species in S Mexico to South America. All are consanguineously polygynous and xylomycetophagous. Key: Wood (1982: 778) for Central America.

***Xylosandrus* Reitter** [1913: 80, 83, Type-species: *Xyleborus morigerus* Blandford, monobasic. Synonym: *Apoxyleborus* Wood 1980: 90, Type-species: *Xyleborus mancus* Blandford, original designation]. Distribution: 8 species in USA to South America, about 32 species in SE Asia to Australia and Africa. All are consanguineously polygynous and xylomycetophagous. Key: Wood (1982: 765) for North and Central America.

***Cnestus* Sampson** [1911: 383, Type-species: *Cnestus magnus* Sampson, monobasic. Synonym: *Tosaxyleborus* Murayama 1950a:

49, Type-species: *Tosaxyleborus pallidipennis* Murayama =*Cnestus murayamai* Schedl, original designation]. Distribution: About 17 species in SE Asia to Indonesia, the Philippines, and Japan. All are consanguineously polygynous and xylomycetophagous. Key: Nunberg (1972: 476).

***Xyleborinus* Reitter** [1913: 79, 83, Type-species: *Bostrichus saxeseni* Ratzeburg, subsequent designation by Swaine 1918: 50]. Distribution: 8 species in North and Central America, at least 4 in South America, at least 20 in SE Asia to Africa. All are consanguineously polygynous and xylomycetophagous. Key: Wood (1982: 842) for North and Central America.

***Mesoscolytus* Broun** [1904: 125, Type-species: *Mesoscolytus inurbanus* Broun, monobasic]. Distribution: 1 species in New Zealand. It is consanguineously polygynous and xylomycetophagous.

***Hadrodemius* Wood** [1980: 94, Type-species: *Xyleborus globus* Blandford, original designation]. Distribution: About 6 species in SE Asia to Indonesia and the Philippines. All are consanguineously polygynous and xylomycetophagous.

***Eccoptopterus* Motschulsky** [1863: 515, Type-species: *Eccoptopterus sexspinosus* Motschulsky =*Scolytus spinosus* Olivier, monobasic. Synonyms: *Platydactylus* Eichhoff 1886: 25, Type-species: *Platydactylus gracilipes* Eichhoff, monobasic; *Eurydactylus* Hagedorn 1909: 733, *Platydactylus gracilipes* Eichhoff, automatic]. Distribution: About 12 species in SE Asia to Australia and adjacent islands, and Africa. All are consanguineously polygynous and xylomycetophagous.

***Schedlia* Browne** [1950: 641, Type-species: *Xyleborus sumatranus* Hagedorn, original designation]. Distribution: 5 species in SE Asia to Indonesia and New Guinea. All are consanguineously polygynous and xylomycetophagous. Key: Browne (1950: 642).

***Coptodryas* Hopkins** [1915a: 10, 54, Type-species: *Coptodryas confusa* Hopkins, original designation. Synonyms: *Microperus* Wood 1980: 94, Type-species: *Xyleborus theae* Eggers, original designation; *Adryocoetes* Eggers, nomen nudum, in Schedl (1952: 371), Type-species: *Adryocoetes nitidus*, nomen nudum, =*Xyleborus pullus* Schedl, no status]. Distribution: About 20 species in SE Asia to Australia and adjacent islands. All are consanguineously polygynous and xylomycetophagous.

***Taphrodasus* Wood** [1980: 95, Type-species: *Xyleborus percorthylus* Schedl, original designation]. Distribution: 3 species in SE Asia to Indonesia. All are consanguineously polygynous and xylomycetophagous.

***Cryptoxyleborus* Schedl** [1937b: 550, Type-species: *Cryptoxyleborus naevus* Schedl, subsequent designation by Schedl 1962a: 103]. Distribution: About 12 species in Malaya. All are consanguineously polygynous and xylomycetophagous.

***Webbia* Hopkins** [1915b: 222, Type-species: *Webbia dipterocarpi* Hopkins, original designation. Synonyms: *Xelyborus* Schedl 1939b, nomen nudum (Browne 1963a: 57); *Pseudowebbia* Browne 1961: 308, Type-species: *Xyleborus trepanicauda* Eggers, original designation; *Prowebbia* Browne 1962b: 208, Type-species: *Prowebbia subuculae* Browne, original designation]. Distribution: About 32 species in SE Asia to Indonesia and the Philippines. All are consanguineously polygynous and xylomycetophagous. Key: Browne (1962b: 210) to the *pabo* group of species.

Tribe Xyloctonini

Xyloctonidae Eichhoff [1878a: 171, Type-genus: *Xyloctonus* Eichhoff, 1872]

DESCRIPTION.—Frons apparently not dimorphic, usually unadorned; eye emarginate to divided; antennal scape elongate, funicle 6- or 7-segmented, club strongly flattened, sutures procurved, present or obsolete, 1 partly septate or not; pronotum asperate on anterior slope, anterior margin usually armed; procoxae contiguous; scutellum large, flat; tarsi retractable into tibial grooves; venter of abdomen moderately to very strongly ascending to meet elytra.

BIOLOGY.—All are apparently monogamous and phloeophagous. The egg galleries are monoramous in *Ctonoxylon* and biramous in *Scolytomimus*. The eggs are deposited individually in niches and sealed in by frass. The larval mines radiate out from the parental gallery and may be rather long.

TAXONOMY.—This is a small group of predominantly African genera that are poorly known. It appears to be a primitive branch of the same phyletic line that gave rise to the

Cryphalini. Together these two tribes appear to occupy a position intermediate between primitive Micracini and Corthylini. A principal distinguishing character of Xyloctonini is their ability to totally withdraw the meso- and metatibiae into tibial grooves. This character is shared by a small group of genera in the Cryphalini that are allied to *Scolytogenes*; thus, tribal placement for them is dependent on the number of segments in the antennal funicle. The limited distribution of this tribe, accompanied by conspicuous anatomical diveristy, makes comments on its antiquity difficult.

Key to the Genera of Xyloctonini

1. Eye entire to feebly emarginate; suture 1 of antennal club septate, almost straight; funicle 7-segmented; elytra declivous behind, abdomen raised only slightly to meet them; interstriae costate; Africa; 1.5-2.1 mm . ***Cryphalomimus***

— Eye moderately emarginate to divided; sutures of antennal club weakly to strongly procurved . . 2

2(1). Eye moderately emarginate, about one-third divided by an emargination; basal (usually) and lateral margins of pronotum rounded; funicle 6-segmented, sutures of antennal club feebly to moderately procurved, 1 not septate; elytral declivity steep, abdomen ascending very slightly; Africa, 1.9-2.6 mm . . . . ***Glostatus***

— Eye more than half divided by an emargination to completely divided; basal and lateral margins of pronotum with a fine, raised line (either continuous or beaded); sutures of antennal club strongly procurved, 1 partly to entirely septate (when sutures reduced septum remains); abdomen moderately to very strongly ascending to meet moderately to feebly declivous elytra 3

3(2). Antennal funicle 7-segmented, club moderately flattened, asymmetrical, comparatively small, about equal in length to scape, suture 1 with posterior half septate; elytral declivity rather steep, abdomen ascending moderately to meet apex; eye always divided; Africa; 1.8-3.6 mm . . . . ***Ctonoxylon***

— Antennal funicle 6-segmented, club strongly flattened, symmetrical, large, conspicuously longer than scape, suture 1 partly septate or not; elytral declivity short, very gradual, abdomen very strongly ascending to meet apex; eye divided or not 4

4(3). Antennal club devoid of sutures except for strongly procurved septum in posterior half of suture 1; scutellum large, flat, subtriangular, its surface flush with that of base of elytra; India to Philippines and Fiji; 1.0-2.4 mm . . . ***Scolytomimus***

— Antennal club with 2 or 3 very strongly procurved sutures, none of them septate; scutellum averaging smaller, subquadrate, adjacent basal area on interstriae 1 and 2 impressed thereby causing scutellum to project slightly dorsad; Africa; 1.3-2.8 mm . . . . ***Xyloctonus***

***Cryphalomimus* Eggers** [1927b: 174, Type-species: *Cryphalomimus striatus* Eggers, monobasic]. Distribution: 3 species in Africa (Congo to East Africa).

***Glostatus* Schedl** [1939d: 386, Type-species: *Glostatus declividepressus* Schedl, monobasic. Synonyms: *Ctonocryphus* Schedl 1941: 398, Type-species: *Ctonocryphus xyloctonus* Schedl, monobasic; *Apoglostatus* Schedl 1957a: 155, Type-species: *Apoglostatus acaciae* Schedl, monobasic; *Paraglostaus* Schedl 1964c: 304, Type-species: *Ctonocryphus nigrivestris* Schedl, original designation; *Rhopalocryphus* Nunberg 1967: 320, Type-species: *Rhopalocryphus seydeli* Nunberg]. Distribution: 16 species in Africa. Apparently all are monogamous and phloeophagous.

***Ctonoxylon* Hagedorn** [1910c: 4, Type-species: *Ctonoxylon auratum* Hagedorn, subsequent designastion by Hopkins 1914: 119, Schedl's (1961: 426) designation is invalid]. Distribution: About 32 species in Africa. Apparently all are monogamous and phloeophagous.

***Scolytomimus* Blandford** [1895: 319, Type-species: *Scolytomimus dilutus* Blandford, monobasic. Synonyms: *Neoxyloctonus* Eggers 1923: 143, Type-species: *Neoxyloctonus philippinensis* Eggers, monobasic; *Scolytocleptes* Schedl 1962f: 490, Type-species: *Scolytomimus maculatus* Beeson, original designation]. Distribution: About 15 species from India and Sri Lanka (Ceylon) to Samoa. All are monogamous and phloeophagous.

***Xyloctonus* Eichhoff** [1872: 134, Type-species: *Xyloctonus scolytoides* Eichhoff, monobasic]. Distribution: 14 species in Africa. All are monogamous and phloeophagous. Key: Menier (1974: 658).

Tribe Cryphalini

Cryphaloidea Lindemann [1876: 165, Type-genus: *Cryphalus* Erichson, 1836]

Trypophloeinae Nüsslin [1911: 373, Type-genus: *Trypophloeus* Fairmaire, 1868]

Ernoporinae Nüsslin [1911: 375, Type-genus: *Ernoporus* Thomson, 1859]

Eidophelinae Murayama [1954: 200, Type-genus: *Eidophelus* Eichhoff, 1875, amended from Eidopherinae by Wood 1978: 114]

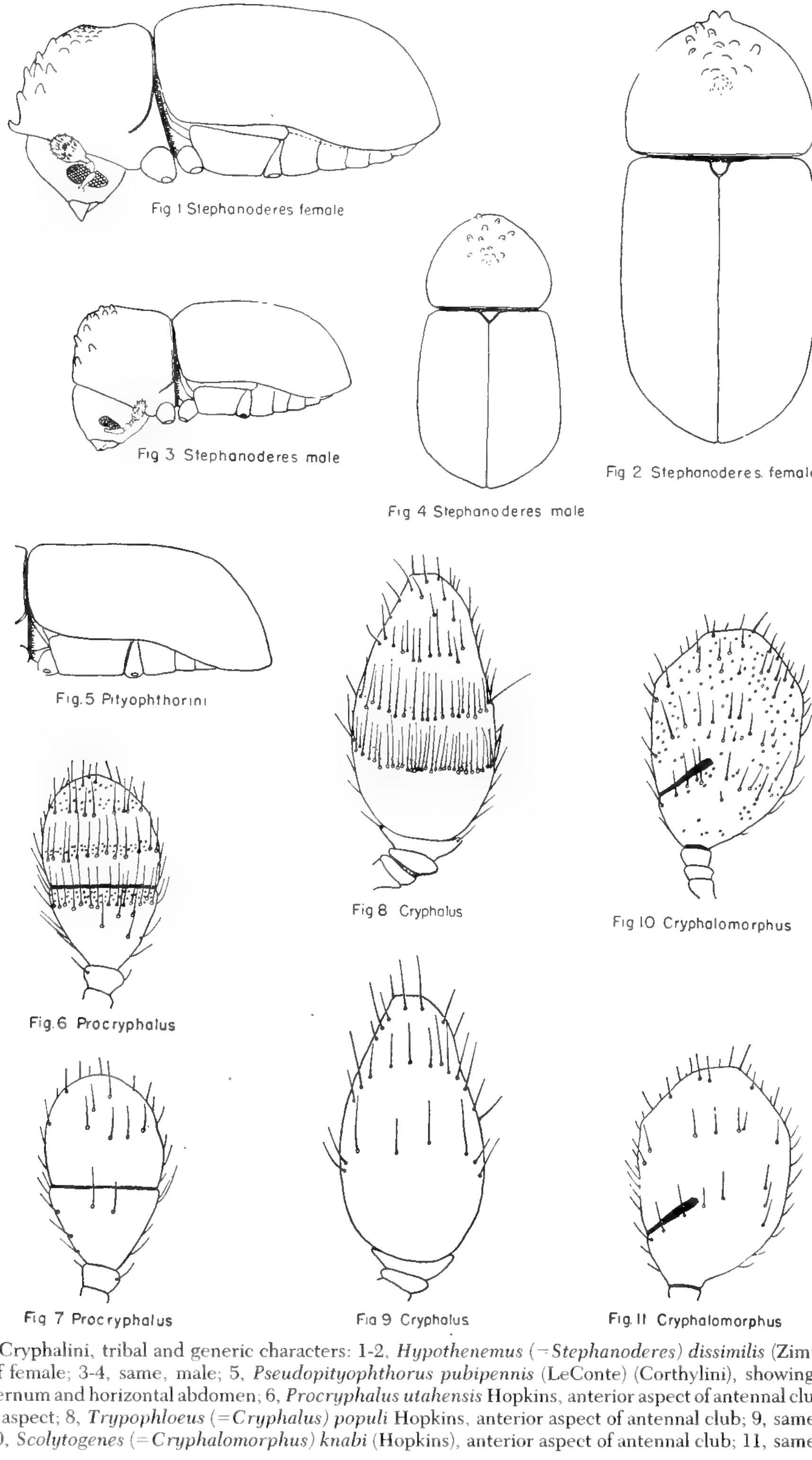


Fig. 53. Cryphalini, tribal and generic characters: 1-2, *Hypothenemus* (=*Stephanoderes*) *dissimilis* (Zimmermann), outline of female; 3-4, same, male; 5, *Pseudopityophthorus pubipennis* (LeConte) (Corthylini), showing consealed metepisternum and horizontal abdomen; 6, *Procryphalus utahensis* Hopkins, anterior aspect of antennal club; 7, same, posterior aspect; 8, *Trypophloeus* (=*Cryphalus*) *populi* Hopkins, anterior aspect of antennal club; 9, same, posterior aspect; 10, *Scolytogenes* (=*Cryphalomorphus*) *knabi* (Hopkins), anterior aspect of antennal club; 11, same, posterior aspect.

DESCRIPTION.—Frons rarely dimorphic, usually convex, usually not adorned; eye usually entire, shallowly emarginate in a few genera; antennal scape elongate, simple, funicle 3- to 5-segmented, club moderately to strongly flattened, sutures present or obsolete, 1 sometimes septate, sutures on posterior face strongly displaced toward apex; pronotum coarsely asperate on anterior slope (Fig. 53), anterior margin usually armed, lateral and basal margins usually (not always) marked by a finely elevated line; procoxae contiguous; tibiae rather strongly flattened, their lateral margins armed by more than four socketed teeth; metepisternal spine usually modified, often partly replaced by a callus or modified groove; scutellum large, flush with adjacent surface of elytra; basal margins of elytra sometimes marked by a fine, raised line; elytral sculpture usually conservative, their costal margins near apex usually ascending at least slightly; venter of abdomen usually rising slightly to meet elytra; vestiture commonly includes scales.

BIOLOGY.—Monogamous, except for consanguineous polygyny in *Hypothenemus*, *Cryptocarenus*, *Periocryphalus*, and *Trischidias*, and either phloeophagous or myelophagous. Mycetophagous in one species of *Hypothenemus*. Parental gallery usually of a cave type, often modified into crude, elongate, brood chambers. The eggs are deposited in clusters, often mixed with frass; definite egg niches have not been reported. The larvae may form individual mines (*Trypophloeus*, *Cryphalus*) or feed in congress as they extend the parental chamber (*Procryphalus*, *Hypothenemus*, etc.). The brood may emerge through individual exit holes or through the parental entrance tunnel, depending upon the larval habit. In temperate areas the winter is most commonly passed in the larval stage; two generations per year is the common habit.

TAXONOMY.—The worldwide distribution and structural diversity of this tribe suggest a pre-Tertiary origin. However, the proliferation of large numbers of species, particularly in *Cryphalus*, indicates that recent, very rapid evolution is in progress. *Trypophloeus*, *Procryphalus*, *Ernoporicus*, and *Cryphalus* appear to have reached North America from Asia rather recently. *Hypothenemus*, *Cryptocarenus*, *Trischidias*, and *Scolytogenes* in North America were recent derivitives from the neotropical realm. The South American element of Cryphalini appears to contain very ancient, endemic elements (*Acorthylus*, *Neocryphus*, *Stegomerus*, *Cryptocarenus*) and more recent arrivals (*Hypothenemus*, *Scolytogenes*). The more recent elements are largely confined to the tropics and are shared with Africa; similarity of species groups suggest a connection of faunas as late as early Tertiary. The main center of distribution for the tribe appears to be in the Oriental and Australian realms. This is also the area where rapid evolution has produced a great abundance of very closely related species. In this area, generic limits are often obscure, whereas in other parts of the world they are quite distinct. This is probably the most poorly known tribe in the world and it is likely to remain so until much more material is available for study.

Key to the Genera of Cryphalini

1. Basal and lateral margins of pronotum rounded; procoxae usually narrowly separated, intercoxal piece continuous (except contiguous and intercoxal piece longitudinally emarginate in *Trypophloeus*, *Stegomerus*, *Acorthylus*) 2

— Basal and usually basal third of lateral margins of pronotum marked by a finely raised line; procoxae either contiguous or narrowly separated; eye entire or narrowly emarginate 8

2(1). Eye shorter, less than twice as long as wide, entire (rarely with a few facets absent suggesting a weak, narrow emargination) 3

— Eye moderately elongate, 2.0 or more times as long as wide, more than half of its anterior margin occupied by a sinuation or broad emargination one-third as deep as width of eye; neotropical genera 6

3(2). Antennal funicle 5-segmented, club slender (1.8 or more times as long as wide), 2 sutures clearly marked, its apex subacutely pointed (Fig. 52), elytral interstriae 10 continuing to apex; North America, N Asia, Europe; *Salix*, *Populus*, *Alnus*; 1.4-2.1 mm ..... ***Trypophloeus***

— Antennal funicle 3- to 5-segmented, club broad (less than 1.3 times as long as wide), its apex rather broadly rounded, suture 1 usually marked, 2 obsolete or nearly so; interstriae 10 obsolete before attaining level of base of abdominal sternum 5 4

4(3). Eye entire; antennal club longer, basal area more strongly flattened, suture 1 straight, septate, 2 obsolete; funicle 4-segmented; female frons not conspicuously pubescent;

North America to NE Asia; *Populus, Salix, Fraxinus*; 1.3-2.2 mm .... ***Procryphalus***

— Eye entire to weakly sinuate; antennal club with sutures procurved or absent, 1 not septate when present 5

5(4). Antennal funicle 4-segmented, club with procurved sutures indicated by rows of setae; E North America, N Asia, Europe; *Fraxinus, Fagus, Cornus*; 1.2-1.7 mm ...... ***Ernoporicus***

— Antennal funicle 3-segmented, club devoid of sutures; NE Asia; *Euonymus*; 1.4 mm .... ***Allernoporus***

6(2). Antennal funicle 5-segmented, club large, subcircular, about as wide as long, sutures conspicuously procurved; discal striae not impressed, poorly defined (punctures often confused); Mexico to South America; vines (lianas); 1.1-1.9 mm .... ***Stegomerus***

— Antennal funicle 3-segmented, club elongate, at least 1.5 times as long as wide; sutures almost straight 7

7(6). Antennal funicle shorter than scape, segments 2 and 3 small, subequal in size; elytral striae impressed, punctures rather coarse; S South America; host unknown; 1.4-1.5 mm .... ***Neocryphus***

— Antennal funicle with segment 2 greatly enlarged, as long as scape; elytral striae not impressed, strial rows usually not distinguishable (at least one exception); South America; *Prunus*, etc.; 1.2-1.8 mm .... ***Acorthylus***

8(1). Basal margin of pronotum marked by a fine, raised line, lateral margin rounded; sutures on antennal club procurved, usually distinct . 9

— Both basal and lateral margins of pronotum marked by a fine, raised line; sutures on antennal club present or absent, variable 12

9(8). Eye emarginate; pronotal asperities confused; antennal grooves or sutures moderately procurved 10

— Eye entire; pronotal asperities arranged in concentric rows; antennal sutures rather strongly to profoundly procurved or obsolete 11

10(9). Antennal funicle 5-segmented, club with sutures 1 and 2 marked by moderately procurved grooves and rows of setae; pronotal asperities coarse, confused; eye conspicuously emarginate; Africa; hosts unknown; 2.0-2.3 mm .... ***Stephanopodius***

— Antennal funicle 4-segmented, club with suture 1 septate and angulate; eye rather small, shallowly emarginate; SE Asia; 1.2-1.6 mm .... ***Coriacephilus***

11(9). Antennal funicle 4-segmented; vestiture of abundant, confused scales; sutures on antennal club very strongly procurved or obsolete; Europe, Asia; *Tilia, Fagus*, etc.; 1.1-1.5 mm .... ***Ernoporus***

— Antennal funicle 3-segmented; vestiture of uniseriate rows of scales on discal interstriae, a few supplemental scales on declivity; sutures on antennal club rather weakly procurved, sometimes obscure; SE Asia; broadleaf trees; 1.1-1.5 mm ...... ***Ernocladius***

12(8). Posterior face of metatibia (usually also mesotibia) with a groove for reception of tarsus on lateral half from apex at least two-thirds of distance toward base, grooved area glabrous, usually with a row of setae along its mesal margin, tibia usually more broadly flattened, gradually tapered on its distal third, with socketed teeth more numerous and distributed over at least apical third (possible confusion with Xyloctonini, except eye entire in these Cryphalini); male subequal in size to female, capable of flight 13

— Metatibia either without groove for reception of tarsus or groove restricted to less than distal one-fifth of tibial length, setae randomly distributed on its lateral half, tibia usually subtruncate apically, socketed teeth usually restricted to apical one-fifth; male either normal or deformed 16

13(12). Antennal club with suture 1 partly septate, suture either straight or strongly procurved, if straight then funicle 3-segmented); body usually stouter, pubescence moderately abundant; groove forming lateral line on pronotum rather poorly defined 14

— Antennal club with suture 1 aseptate (or obscurely septate, if suture present then funicle 4-segmented; body rather slender, elytral vestiture sparse, largely confined to declivity; groove forming lateral and basal raised line on pronotum rather strongly impressed 15

14(10). Antennal funicle 3-segmented, club with sutures 1 and 2 weakly procurved, clearly marked by setae, 1 also grooved and partly septate; venter of abdomen horizontal; India to Sri Lanka (Ceylon); *Euphorbia*; 1.0-1.3 mm .... ***Cryphalogenes***

— Antennal funicle 4-segmented, club with sutures strongly to profoundly procurved, 1 marked on mesal half by a septum, remaining sutures marked by setae or obsolete (septum complete in several small New Guinea species); venter of abdomen weakly to very strongly ascending to meet apex of elytra, apex of elytra usually ascending also; pantropical; hosts usually lianas; 1.0-2.5 mm .... ***Scolytogenes***

15(13). Antennal club with sutures 1 and 2 weakly procurved and clearly marked by rows of setae, 1 also grooved; basal half of pronotum reticulate or minutely rugose, punctures small to obsolete; Micronesia; hosts unknown; 1.1-1.4 mm .... ***Hemicryphalus***

— Antennal club with sutures entirely obsolete; basal half of pronotum smooth, shining, with a few coarse punctures; India and E USSR to Japan; *Phellodendron*; 1.2-1.3 mm . ***Eidophelus***

16(12). Tarsal segment 3 rather broad, bilobed; procoxae narrowly separated, intercoxal piece not longitudinally emarginate; eye emarginate; antennal club with aseptate sutures clearly marked by grooves and setae 17

— Tarsal segment 3 narrow, often laterally compressed, not bilobed; procoxae contiguous, intercoxal piece longitudinally emarginate or partly absent 18

17(16). Antennal funicle 5-segmented, sutures on club weakly to rather strongly procurved; phloeophagous in broadleaf trees; pantropical; 1.1-2.8 mm .... ***Hypocryphalus***

— Antennal funicle 4-segmented, sutures on club recurved (occasionally weakly procurved); phloeophagous in broadleaf and coniferous hosts; E Hemisphere, North America (1 dubious record from South America); 1.0-2.8 mm .... ***Cryphalus***

18(16). Antennal funicle 3-segmented, club with or without sutures, never with a septum; male normal, not dwarfed or flightless 19

— Antennal funicle 3- to 5-segmented, sutures always indicated on club, 1 frequently partly septate; male dwarfed, flightless 21

19(18). Antennal club with moderately procurved sutures clearly marked by grooves and rows of setae; eye emarginate; striae obsolete, punctures on disc confused; SE Asia to Philippines; 0.8-1.3 mm .... ***Margadillius***

— Antennal club without indications of grooves or rows of setae; eye entire; strial punctures in recognizable rows 20

20(19). Anterior margin of pronotum armed by 0-6 serrations, asperities on anterior half of pronotum larger, less numerous; body stouter, 1.4-2.0 times as long as wide; frons convex to flattened in both sexes; SE Asia to Hawaii; 0.8-1.8 mm .... ***Ptilopodius***

— Anterior margin of pronotum armed by 10-16 serrations, asperities smaller, much more numerous, often extending to base; body more slender, 2.5-2.6 times as long as wide; female frons rather narrowly impressed; SE Asia and Indonesia to Micronesia; 1.3-1.5 mm .... ***Cosmoderes***

21(18). Antennal funicle 3- to 5-segmented, club with or without sutures, when funicle 3-segmented then club always with suture 1 partly septate 22

— Antennal funicle 3-segmented, club never septate, sutures sometimes marked by rows of setae; body rather stout, 2.0-2.3 times as long as wide; very small 23

22(21). Anterior margin of pronotum armed by 10-16 serrations; antennal funicle 5-segmented, club never septate, sutures marked by rows of setae; mature body color yellowish to reddish brown; vestiture usually very sparse (rare exceptions); myelophagous; tropical America (1 introduced to Africa); 1.4-3.3 mm .... ***Cryptocarenus***

— Anterior margin of pronotum usually armed by 1-8 serrations; antennal funicle 3- to 5-segmented, when 5-segmented then suture 1 of club partly septate; antennal club clearly marked by sutures; mature color usually darker, vestiture more abundant; phloeophagous, myelophagous, spermophagous, 1 mycetophagous, worldwide in tropical and warm temperate areas; 0.6-2.8 mm .... ***Hypothenemus***

23(21). Antennal club with sutures clearly marked by rows of setae; eye entire; phloeophagous in trees and shrubs; E North America to Mexico and Hawaii; 0.6-1.1 mm .... ***Trischidias***

— Antennal club without indications of sutures; eye emarginate; myelophagous in vines; South America; 0.8-1.1 mm ... ***Periocryphalus***

Trypophloeus **Fairmaire** [1868: 105, Type-species: *Bostrichus binodulus* Ratzeburg, monobasic. Synonym: *Glyptoderus* Eichhoff 1878a: 34, 44, 137, Type-species: *Bostrichus binodulus* Ratzeburg, subsequent designation by Hopkins 1914: 122]. Distribution: 4 species in North America, about 12 in N Asia and Europe. All are monogamous and phloeophagous. Keys: Wood (1954b: 989, 1982: 851) for North America, Reitter (1913: 69), Balachowsky (1949: 214), Stark (1952: 281) for Europe and Asia.

Procryphalus **Hopkins** [1915a: 7, 33, Type-species: *Procryphalus populi* Hopkins = *Cryphalus mucronatus* LeConte, original designation]. Distribution: 2 species in North America (in *Populus*, *Salix*), 1 in NE Asia (Ussuri, in *Fraxinus*). All are monogamous and phloeophagous. Key: Wood (1954b: 982, 1982: 859) for North America.

Ernoporicus **Berger** [1917: 242, Type-species: *Ernoporicus spessivtzevi* Berger, monobasic. Synonyms: *Eocryphalus* Kurentzov 1941: 161, 230, Type-species: *Eocryphalus semenovi* Kurentzov, monobasic; *Ernopocerus* Balachowsky 1949: 211, Type-species: *Ernoporus caucasicus* Lindemann, subsequent designation by Wood 1954b: 986]. Distribution: 1 species in North America (West Virginia), about 12 in Europe and Asia. All are apparently monogamous and phloeophagous. Keys: Balachowsky (1949: 211), Reitter (1913: 68), Stark (1952: 271).

Allernoporus **Kurentzov** [1941: 159, Type-species: *Allernoporus euonymi* Kurentzov, monobasic]. Distribution: 1 species in NE Asia (in *Euonymus*). It apparently is monogamous and phloeophagous.

***Stegomerus* Wood** [1967: 129, Type-species: *Stegomerus vulgaris* Wood, original designation]. Distribution: 5 species in Mexico and Central America, 1 in South America (Venezuela). All are monogamous and phloeophagous. Keys: Wood (1967: 130, 1982: 855).

***Neocryphus* Nunberg** [1956a: 139, Type-species: *Neocryphus argentinensis* Nunberg, original designation]. Distribution: 2 species in South America (Argentina).

***Acorthylus* Brèthes** 1922a: 304, Type-species: *Acorthylus asperatus* Brèthes, monobasic. Synonym: *Phacrylus* Schedl 1938a: 24, Type-species: *Phacrylus bosqui* Schedl, monobasic]. Distribution: About 5 species in South America. All are monogamous and phloeophagous.

***Stephanopodius* Schedl** [1941: 396, Type-species: *Stephanoderes dispar* Eggers, subsequent designation by Schedl 1961: 633. Synonyms: *Cryphalomimus* Browne 1962a: 75, Type-species: *Hypocryphalus ghanaensis* Schedl, original designation, preoccupied; *Cryphalomimetes* Browne 1963b: 242, Type-species: *Hypocryphalus ghanaensis* Schedl, automatic]. Distribution: About 7 species in Africa.

***Coriacephilus* Schedl** [1939b: 339, Type-species: *Stephanoderes coriaceus* Eichhoff, original designation]. Distribution: About 4 species in SE Asia to Philippines.

***Ernoporus* Thomson** [1859: 147, Type-species: *Bostrichus tiliae* Panzer, original designation. Synonyms: *Cryphalops* Reitter 1889: 94, Type-species: *Cryphalus lederi* Reitter =*Bostrichus tiliae* Panzer, monobasic; *Stephanorhopalus* Hopkins 1915a: 35, Type-species: *Stephanorhopalus melodori* Hopkins, original designation (specific name of type-species validly amended by Schedl 1966a: 19); *Euptilius* Schedl 1940b: 589, Type-species: *Ernoporus concentralis* Eggers, original designation]. Distribution: At least 13 and perhaps 20 species in Europe and S Asia to the Philippines. All are monogamous and phloeophagus.

***Ernocladius* Wood** [1980: 93, Type-species: *Cryphalus corpulentus* Sampson, original designation]. Distribution: About 4 species in S Asia to Sri Lanka (Ceylon).

***Cryphalogenes* Wood** [1980: 91, Type-species: *Cryphalogenes euphorbiae* Wood, original designation]. Distribution: 4 species in India to Sri Lanka (Ceylon) in *Euphorbia*. All are monogamous and excavate dying tissue immediately under the epidermis.

***Scolytogenes* Eichhoff** [1878a: 475, 497, 1878b: 387, Type-species: *Scolytogenes darwini* Eichhoff, monobasic. Synonyms: *Lepicerus* Eichhoff 1878a: 476, 501, Type-species: *Lepicerus aspericollis* Eichhoff, monobasic; *Cryphalomorphus* Schaufuss 1890: 12, Type-species: *Cryphalomorphus communis* Schaufuss, monobasic; *Letznerella* Reitter 1913: 68, Type-species: *Bostrichus jalapae* Letzner, monobasic; *Hypothenoides* Hopkins 1915a: 7, 11, Type-species: *Hypothenoides parvus* Hopkins, original designation; *Ernoporides* Hopkins 1915a: 8, 34, Type-species: *Ernoporides floridensis* Hopkins =*Ernoporides knabi* Hopkins, original designation; *Neocryphalus* Eggers 1922: 169, Type-species: *Neocryphalus usagaricus* Eggers, monobasic; *Negritus* Eggers 1923: 141, Type-species: *Negritus ater* Eggers, designated by Wood 1982: 861; *Cylindrotomicus* Eggers 1936: 633, Type-species: *Cylindrotomicus squamulosus* Eggers, monobasic; *Lepicerinus* Hinton 1936: 473, Type-species: *Lepicerus aspericollis* Eichhoff, automatic; *Xylocryptus* Schedl 1975c: 352, Type-species: *Xylocryptus papuanus* Schedl, original designation]. Distribution: 7 species in North and Central America; about 60 in other tropical and subtropical areas around the world. All are monogamous and almost all bore in the stems of vines (lianas). Key: Wood (1960: 27) for Micronesia, (1982: 862) for North and Central America.

***Hemicryphalus* Schedl** [1963b: 264, Type-species: *Eidophelus argutus* Wood, original designation]. Distribution: 3 species in Micronesia (W Pacific Islands). Key: Wood (1960a: 32).

***Eidophelus* Eichhoff** [1875: 200, Type-species: *Eidophelus imitans* Eichhoff, monobasic. Synonym: *Phellodendrophagus* Krivolutskaya 1958: 150, Type-species: *Phellodendrophagus elegans* Krivolutskaya, monobasic]. Distribution: About 8 species in SE Asia and Indonesia.

***Hypocryphalus* Hopkins** [1915a: 8, 41, Type-species: *Hypocryphalus rotundus* Hopkins, original designation. Synonym: *Dacryphalus* Hopkins 1915a: 8, 42, Type-species:

Dacryphalus obesus Hopkins, original designation]. Distribution: About 47 species in Africa, S Asia to Australia and Samoa; 1 introduced into America (*mangiferae*, in *Mangifera indica*). All apparently are monogamous and phloeophagous.

Cryphalus **Erichson** [1836: 61, Type-species: *Bostrichus asperatus* Gyllenhal, subsequent designation by Thomson 1859: 147, lectotype for type-species designated by Wood 1972: 41. Synonyms: *Pseudocryphalus* Ferrari 1869: 252, Type-species: *Bostrichus sidneyanus* Nordlinger, monobasic; *Taenioglyptes* Bedel 1888: 398, Type-species: *Bostrichus abietus* Ratzeburg =*Bostrichus asperatus* Gyllenhal, original designation; *Cryptarthrum* Blandford 1896b: 200, Type-species: *Cryptarthrum walkeri* Blandford, monobasic; *Allarthrum* Hagedorn 1912: 355, Type-species: *Allarthrum kolbei* Hagedorn, monobasic; *Ericryphalus* Hopkins 1915a: 8, 38, Type-species: *Ericryphalus henshawi* Hopkins =*Hypothenemus sylvicola* Perkins, original designation; *Piperius* Hopkins 1915a: 8, 39, Type-species: *Piperius pini* Hopkins =*Hypothenemus sylvicola* Perkins, original designation; *Ernocryphalus* Murayama 1958: 934, Type-species: *Ernocryphalus birosimensis* Murayama, original designation; *Acryphalus* Tsai & Li 1963: 604, 622, Type-species: *Cryphalus lipingensis* Tsai & Li, designated by Wood 1984: 224; *Jugocryphalus* Tsai & Li 1963: 602, 622, Type-species: *Cryphalus piceus* Eggers, designated by Wood 1984: 224]. Distribution: 3 species in North America, 1 dubious record from South America, 11 in Africa, about 7 in Europe, more than 200 nominate species have been reported from Asia to Australia and adjacent islands. All are monogamous and phloeophagous. Keys: Reitter (1913: 66) for Europe, Balachowsky (1949: 206) for France, Stark (1952: 254) for USSR, Wood (1954b: 1002, 1982: 867) for North America and (1960a: 23) for Micronesia.

Margadillius **Hopkins** [1915a: 8, 37, Type-species: *Margadillius margadilaonis* Hopkins, original designation]. Distribution: About 9 species in SE Asia, Philippines, New Guinea, and Indonesia. The true status and extent of this genus have not been established. Key: Hopkins (1915a: 37).

Ptilopodius **Hopkins** [1915a: 7, 11, Type-species: *Ptilopodius stephegynis* Hopkins, original designation]. Distribution: 15 species in Africa, SE Asia, and adjacent islands have been assigned to this genus, some erroneously. Key: Wood (1960a: 18) for Micronesia.

Cosmoderes **Eichhoff** [1878a: 495, Type-species: *Cosmoderes monilicollis* Eichhoff, monobasic. Synonyms: *Erioschidias* Schedl 1938b: 42, Type-species: *Cryphalus setistriatus* Lea, subsequent designation by Wood 1960a: 21; *Dendriops* Schedl 1953b: 125, Type-species: *Dendriops granulicollis* Schedl, monobasic; *Vitaderes* Beeson 1941: 301, nomen nudum, Type-species: *Vitaderes luffa*, nomen nudum =*Cosmoderes monilicollis* Eichhoff, no status]. Distribution: About 22 species in Africa to SE Asia and Australia. At least 2 species were taken from lianas.

Cryptocarenus **Eggers** [1937: 79, Type-species: *Cryptocarenus diadematus* Eggers, original designation. Synonym: *Tachyderes* Blackman 1943a: 35, Type-species: *Tachyderes floridensis* Blackman =*Cryptocarenus seriatus* Eggers, original designation]. Distribution: 5 species in North and Central America, more than 7 in South America, 1 introduced into tropical Africa. All are consanguineously polygynous and primarily myelophagous. Key: Wood (1982: 912).

Hypothenemus **Westwood** [1836: 34, Type-species: *Hypothenemus eruditus* Westwood, monobasic. Synonyms: *Stephanoderes* Eichhoff 1872: 132, Type-species: *Stephanoderes chapuisii* Eichhoff =*Crypturgus dissimilis* Zimmermann, subsequent designation by Hopkins 1914: 130; *Homoeocryphalus* Lindemann 1876: 168, Type-species: *Stephanoderes ehlersii* Eichhoff =*Hypothenemus eruditus* Westwood, monobasic; *Adiaeretus* Hagedorn 1909: 744, Type-species: *Adiaeretus spinosus* Hagedorn =*Stephanoderes elaphus* Eichhoff, monobasic; *Stylotentus* Schedl 1939b: 380, Type-species: *Hypothenemus concolor* Hagedorn, subsequent designation by Schedl 1961: 4, 48; probable synonym, *Triarmocerus* Eichhoff 1878a: 42, 119, Type-species: *Triarmocerus cryphaloides* Eichhoff, monobasic, type lost; *Chondronoderes* Schedl 1940b: 589, Type-species: *Stephanoderes magnus* Eggers, monobasic; *Archeo-*

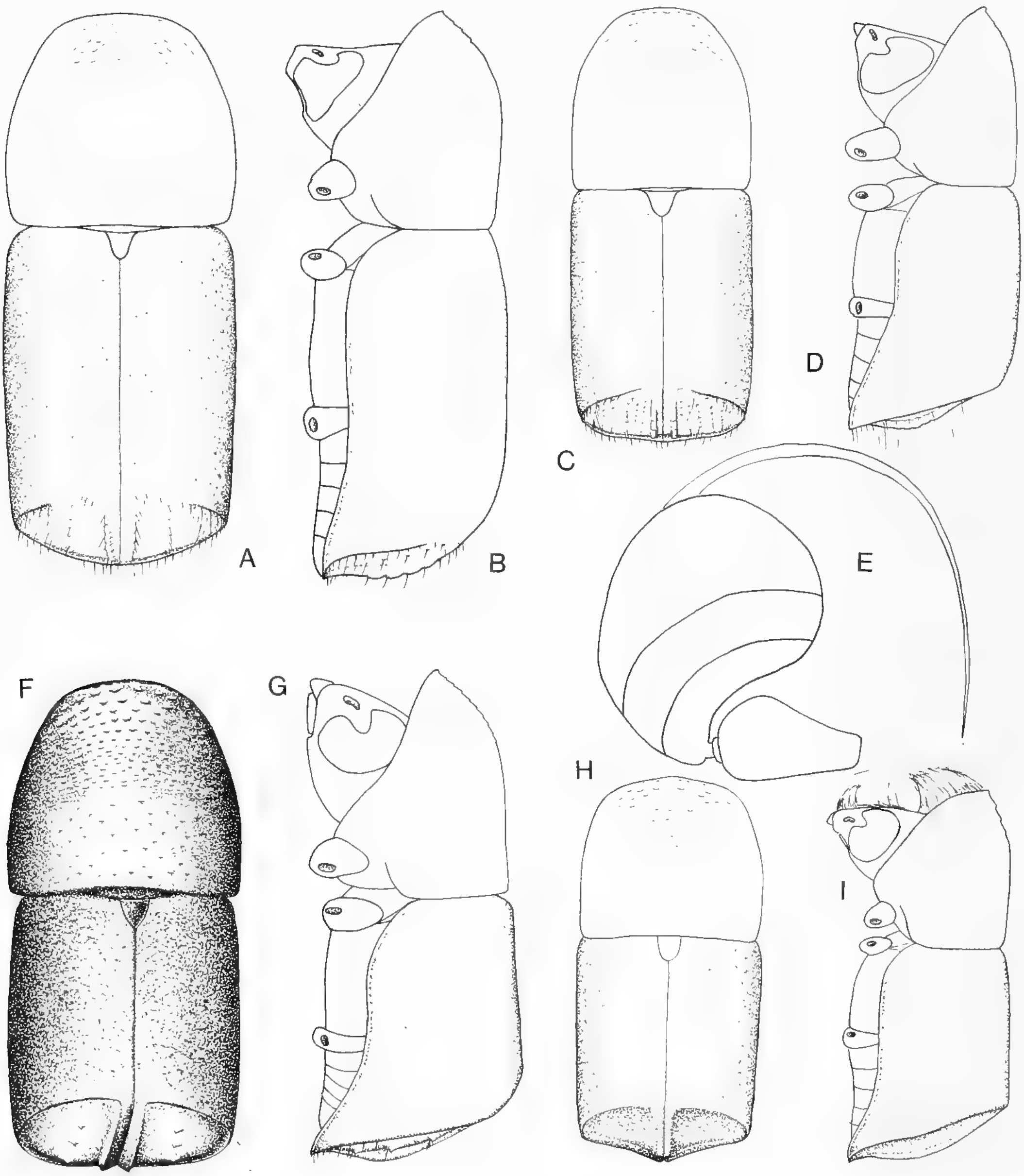


Fig. 54. *Corthylus* spp. (Corthylini): A-B, *subserratus* Wood; C-E, *serratus* Wood; F-G, *concisus* Wood; H-I, *procerus* Bright.

phalus Schedl 1941: 392, Type-species: *Archeophalus natalensis* Schedl, monobasic; *Pachynoderes* Schedl, 1941: 393, Type-species: *Pachynoderes deprecator* Schedl, monobasic; *Lepiceroides* Schedl 1957a: 59, Type-species: *Lepiceroides aterrimus* Schedl, monobasic; *Ernophloeus* Nunberg 1958: 484, Type-species: *Ernophloeus costalimai* Nunberg =*Stephanoderes sundaensis* Eggers, original designation; *Epsips* Beeson 1941: 287, nomen nudum, Type-species: *Epsips sylvarum*, nomen nudum, no status]. Distribution: 39 species in North and Central America; several hundred nominate species from other tropical and subtropical areas have been assigned to this genus, but a majority of them are now in synonymy. All are consanguineously polygynous and myelophagous,

phloeophagous, or spermophagous. Keys: Wood (1954: 1017, 1052, 1982: 876) for North and Central America.

***Trischidias* Hopkins** [1915a: 7, 12, Type-species: *Trischidias georgiae* Hopkins, original designation]. Distribution: 4 species in SE North America to Mexico, 1 imported to Hawaii. All are consanguineously polygynous and phloeophagous. Keys: Wood (1954b: 1067, 1982: 872).

***Periocryphalus* Wood** [1971: 33, Type-species: *Periocryphalus pullus* Wood, original designation]. Distribution: 2 species in South America. Both are consanguineously polygynous and myelophagous in minute lianas.

Tribe Corthylini

Corthyli LeConte [1876: 346, 347, Type-genus: *Corthylus* Erichson, 1836]

Pityophthoridae Eichhoff [1878a: 173, Type-genus: *Pityophthorus* Eichhoff, 1864]

Araptidae Eichhoff [1878a: 305, Type-genus: *Araptus* Eichhoff, 1872]

Amphicranidae Eichhoff [1878a: 460, Type-genus: *Amphicranus* Erichson, 1836]

DESCRIPTION.—Frons usually dimorphic, either or both sexes feebly to strongly modified in sculpture and ornamentation; eye emarginate; scape usually elongate, strongly flattened in some *Corthylus* (Fig. 54), etc., funicle 1- to 5-segmented, club strongly flattened, sutures present or obsolete, frequently 1 and/or 2 septate; when present, sutures on posterior face little if any displaced toward apex; anterior slope of pronotum asperate (one exception in female *Corthylus cecropii*), anterior margin frequently armed, lateral and basal margins frequently marked by a fine, raised line; procoxae contiguous, tibiae rather slender, their lateral margins rarely armed by more than four socketed teeth; metepisternal spine obsolete, replaced by small, transverse groove (Fig. 32), thus making it possible for elytra in locked position to cover at least posterior two-thirds of metepisternum (Figs. 53-54); vestiture usually hairlike, scales rarely present.

BIOLOGY.—Monogamy and heterosanguineous polygyny are common throughout the tribe; a few species of *Araptus* practice consanguineous polygyny. Phloeophagy predominates in temporate areas, xylomycetophagy in tropical areas, although myelophagy and spermophagy are common. Parental galleries may be monoramous, biramous, or variously multiramous. The eggs are deposited in niches or, in *Corthylus*, in fully formed larval cradles. The larvae form individual mines or cradles depending on the food habit. The domicile parasitic habit is known in *Corthylocurus*, *Tricolus*, amd *Amphicranus*.

TAXONOMY.—Except for two small endemic genera in Madagascar (*Pityodendron*, *Sauroptilius*) and one in Africa (*Mimiocurus*), a few primitive *Pityophthorus* species in Africa, and several modern *Pityophthorus* in Eurasia, obviously derived from North America, this large, unique tribe is entirely American. The occurrence of primitive elements of ancient origin in Africa and Madagascar suggests that basic tribal characters formed prior to or early in the Tertiary. The elytral locking mechanism and antennal club are unique in the family, with the Cryphalini possibly forming an intermediate step between Corthylini and the primitive tribes of Scolytinae.

On a biological basis, the tribe is readily divisible into the phloeophagous Pityophthorina and the xylomycetophagous Corthylina, although anatomical characters to support that division are less definite. The tribe obviously originated in South America and was affected by two radiations. The first occurred prior to the Tertiary and carried a few species into Madagascar and Africa, while those land masses were either connected or close enough for island hopping, and took several species over the land bridge to North America, where a minor secondary radiation occurred. The second major radiation occurred in South America during the Tertiary and produced the Corthylina. *Gnathotrichus* might have reached Central America or southern Mexico over the pre-Tertiary land bridge just prior to or during the early stages of its closure. A few genera and species have reached North America over the present post-Tertiary land bridge or by island hopping in recent time. The occurrence of *Gnatharus*, a member of the Corthylina, in China is more difficult to explain.

The South American element of this tribe is one of the more poorly known segments of the Scolytidae. Much remains to be learned about this remarkable group. *Chiloxylon* Schedl (see Dryocoetini) could belong to this tribe.

Key to the Genera of Corthylini
(Modified from Wood 1982)

1. Phloeophagous, myelophagous, or spermophagous; antennal funicle 5-segmented (except 3- or 4-segmented in *Dendroterus*, *Dacnophthorus*, and some *Pityophthorus costatus*), club usually smaller, symmetrical; prosternal intercoxal piece acutely pointed (except obsolete in *Dacnophthorus*); pubescence usually more abundant, usually in rows on elytra; elytral declivity mostly convex to bisulcate, armature conservative (subtribe Pityophthorina) 2

— Xylomycetophagous; antennal funicle 1- to 5-segmented, club usually much larger, commonly asymmetrical; prosternal intercoxal piece absent (except obtuse in *Gnathotrichus*, *Gnathotrupes*); pubescence usually greatly reduced to obsolete or minute and strongly confused (not in rows); elytral declivity convex to truncate to deeply excavated (weakly bisulcate in some *Gnathotrichus*), commonly with spinelike processes (subtribe Corthylina) 17

2(1). Basal and lateral margins of pronotum rounded, devoid of a fine, raised line; elytra rather coarsely punctured (American genera), or very finely punctured (African genus), unarmed declivity steep, in American genera usually subvertical and somewhat flattened on lower half, almost never bisulcate; discal vestiture abundant 3

— Basal and usually lateral margins of pronotum marked by a finely raised line; elytral declivilty usually more gradual, convex to bisulcate, often ornamented by granules or small denticles 6

3(2). Antennal club pubescent to base, unmarked by sutures, funicle 5-segmented; female frons ornamented by a brush of long hair, male usually with a median tubercle or longitudinal carina at upper level of eyes; elytral declivity conservatively sculptured, usually convex; Africa to India and China; 1.4-2.8 mm . . . . ***Mimiocurus***

— Antennal club with sutures clearly indicated; American genera 4

4(3). Antennal funicle 3- or 4-segmented, club with sutures at least slightly recurved, aseptate; elytral vestiture hairlike; female epistoma not emarginate, mandible never with projecting spines; strong, transverse frontal carina at upper level of eyes, when present, a female character; phloeophagous; SW USA to Panama; *Bursera*, 1 species in *Jatropha*; 1.3-2.9 mm . . . . ***Dendroterus***

— Antennal funicle 5-segmented; secondary sexual characters different 5

5(4). Antennal club with aseptate sutures strongly procurved; interstrial setae scalelike; male frons strongly, transversely carinate at upper level of eyes, female epistoma deeply emarginate to accommodate a pair of mandibular spines; phloeophagous; Costa Rica to Bolivia and Brazil; *Astronium*, *Spondias*; 1.3-1.6 mm . . . . ***Styphlosoma***

— Sutures of antennal club straight or recurved; female epistoma entire, male frons without a transverse carina; mandibular spines never present; elytral declivity convex, interstriae unarmed by tubercles or spines; female frons shallowly concave, bearing a brush of hair, armed on median fourth above eyes by an acute, transverse carina and by a pair of coarse tubercles in lateral areas at level of antennal insertion; male frons convex, simple; Mexico; *Bursera*; 1.6-1.8 mm . . . . ***Phloeoterus***

6(2). Sutures of antennal club moderately to very strongly procurved, only suture 1 septate, or if all external sutures obsolete then mesal half of suture 1 marked internally by a strongly procurved septum at least on 1 side; phloeophagous, myelophagous, spermophagous; S USA to Argentina; 1.1-3.3 mm . . . . ***Araptus***

— Sutures 1 and 2 clearly, equally marked by rows of setae and grooves, straight to moderately procurved, if procurved then both sutures at least partly septate (sutures always straight when both almost obsolete) 7

7(6). Lateral margins of pronotum rounded, without a fine, raised line 8

— Lateral margins of pronotum subacute, marked by a fine, raised line (rather obscure in *Spermophthorus* and some *Pityophthorus* having pronotal asperieies in subconcentric rows 12

8(7). Sutures 1 and 2 of antennal club aseptate and clearly marked by grooves and rows of setae; pronotal asperities continuing in lateral areas to base; larger species; spermophagous in cones of *Pinus*, at least 2 species sometimes myelophagous; North America; 2.2-4.1 mm . . . . ***Conophthorus***

— Sutures 1 and 2 both partly to completely septate or, if aseptate, then antennal club largely glabrous or body size much smaller; pronotal asperities not extending to basal margin; smaller species, not found in cones of conifers 9

9(8). Antennal club rather large, at least 2.5 times as long as funicle; monogamous species 10

— Antennal club comparatively small, less than 1.5 times as long as funicle; polygynous species 11

10(9). Body stouter, 2.5-2.8 times as long as wide; elytral declivity convex; anterolateral areas of female pronotum with a pair of large, oval, densely pilose areas; antennal club with only 2 sutures; phloeophagous, larval mines resemble cradles (of ambrosia beetles); S USA to Honduras; *Pinus*; 1.5-3.2 mm . . . . . ***Pityoborus***

— Body very slender, 3.7-3.8 times as long as wide; elytral declivity strongly impressed; fe-

male pronotum without special pilose areas; antennal club with suture 3 indicated by a row of setae; phloeophagous, but with fungal mycelium in parental gallery; Mexico to South America; *Clematis* and Bignoniaceae vines; 1.2-2.0 mm . . . . ***Dacnophthorus***

11(9). Female pregula very greatly enlarged and bearing a rather dense, conspicuous tuft of very long hair, male pregula only slightly enlarged, usually without tuft of hair; phloeophagous; USA (Arizona, New Mexico); *Pinus*; 1.3-1.8 mm . . . . ***Pityotrichus***

— Female oral region abnormally broad and, usually, with mandibles greatly enlarged; pregula normal; phloeophagous; Central and South America; *Dacreoides*, *Cedrela*, *Protium*; 1.3-1.8 mm . . . . ***Gnatholeptus***

12(7). Pronotum weakly declivous on anterior fourth, asperities small, numerous, gradually decreasing in size toward base; head unusually wide, mandibles large and stout in both sexes; eye large, coarsely faceted, one-third divided by a broad emargination; Madagascar; 3.2-3.4 mm . . . . ***Pityodendron***

— Pronotum more strongly declivous in front, asperities usually not present behind summit; head and mandibles normal 13

13(12). Pronotum without a transverse impression behind summit, transition between asperate and smooth areas more gradual, asperities always confused; interstrial bristles usually stout to scalelike (1 exception, also, almost glabrous in *Sauroptilius*); tropical species . . 14

— Pronotum almost always with a distinct, transverse impression behind summit, if doubtful then asperities almost always arranged in concentric rows; interstrial setae hairlike (if stout then pronotal asperities concentric) 16

14(13). Anterior margin of pronotum unarmed; declivity very broadly excavated (as wide as body), its lateral crests profoundly elevated and serrate, but abruptly ending before sutural apex; Madagascar; 3.2 mm . . . ***Sauroptilius***

— Anterior margin of pronotum armed by serrations or a continuous costa; declivity convex to moderately sulcate, impression rarely equal to more than half width of body; neotropical 15

15(14). Strial punctures rather coarse, mostly in rows, declivity moderately to rather strongly impressed, lateral margins armed or not; frons never armed; epistomal margin with a small, median, premandibular lobe; polygynous; phloeophagous, axes of tabular nuptial chamber perpendicular to cambium, longest axis parallel to grain of wood; Colombia, Venezuela; broadleaf trees; 1.3-3.1 mm . . . . ***Phelloterus***

— Strial punctures either very small or confused; declivity not as steep, convex to shallowly impressed, lateral margins never armed; male frons armed; spermophagous; Central and South America; *Caesalpinus*, etc.; 1.3-1.9 mm . . . . ***Spermophthorus***

16(13). Sutures of antennal club moderately procurved, segment 1 shorter than 2 or 3; greater frontal pubescence a male character; elytral punctures very fine, usually confused, short pubescence abundant, often scalelike; striae usually obsolete; phloeophagous, monogamous; North America to Colombia, China; *Quercus*, rarely other hosts; 1.2-2.6 mm . . . . ***Pseudopityophthorus***

— Sutures of antennal club straight to modestly procurved, segments 1 and 2 subequal in length; pubescence usually much less abundant, never scalelike, strial punctures in rows or, if confused, then rather coarse; phloeophagous, monogamous or heterosanguineously polygynous; America, Europe, Asia, Africa; coniferous and broadleaf hosts; 0.9-3.9 mm . . . . ***Pityophthorus***

17(1). Antennal funicle 5-segmented, club always symmetrical, with 2 or 3 clearly marked sutures; protibia widest near its apex, its posterior face usually flat, unarmed (a few minute granules in some *Gnathotrupes*); elytral declivity conservatively sculptured (except in some *Gnathotrupes*) 18

— Antennal funicle 1- to 4-segmented, club commonly asymmetrical, often greatly enlarged, sutures often reduced or absent; tibiae variously sculptured 19

18(17). Sutures of antennal club straight to moderately procurved, segment 1 not noticeably reduced in size; elytral declivity convex to narrowly, rather shallowly sulcate, subapical margin near apex acutely elevated, sutural apex entire, rather narrowly rounded behind; monogamous; North and Central America; coniferous and broadleaf hosts; 2.0-4.3 mm . . . . ***Gnathotrichus***

— Sutures of antennal club moderately to strongly procurved, segment 1 distinctly smaller; elytral declivity moderately to strongly flattened; elytral apex at least weakly divaricate, very broadly rounded to shallowly emarginate behind, without a submarginal costa near apex; monogamous; Central and South America; broadleaf hosts; 1.3-4.0 mm . . . . ***Gnathotrupes***

19(17). Antennal funicle 2- to 4-segmented, club with 2 sutures clearly marked; elytral apex divaricate (except *Metacorthylus*, *Glochinocerus*), commonly explanate, declivity often elaborately excavated and armed by spines; protibia always slender, with posterior face inflated and tuberculate; body usually slender 20

— Antennal funicle 1-segmented, club with 1, 2, or no sutures; elytral apex entire (except *Brachyspartus*, *Corthylus emarginatus*), declivity convex to rather weakly excavated, never explanate; posterior margin of protho-

racic precoxal piece transversely straight, not extended between coxae; protibia variable; body comparatively stout 24

20(19). Procoxae contiguous, anterior wall of combined cavities and precoxal piece transversely straight (longitudinally very thin); protibia similar in male and female, with a longitudinal marginal row of tubercles, posterior face either unarmed or with a longitudinal row of up to about 4 tubercles; posterior face of female antennal club with long hair sparse to absent; antennal funicle usually 3-segmented, less commonly 2-segmented; frons commonly with a sharply defined granular area 21

— Prothoracic precoxal piece moderately large, posteriorly angulate, occupying anterior portion of area between coxae (except in *Gnatharus*, from Tibet, a thin, transverse partition); male protibia armed by coarse marginal serrations and a row of equally coarse serrations on posterior face, female protibia with posterior face moderately inflated and armed by numerous, confused, small tubercles in addition to coarser marginal row; posterior face of female antennal club ornamented by more abundant, long hair; frons never ornamented by a sharply defined granulate area 22

21(20). Elytra broadly rounded behind, posterior margin of declivity feebly if at all explanate, weakly if at all divaricate; lateral margins of declivity armed by as many as 3 pairs of spines; antennal club oval to subtriangular, little if any longer than wide; anteroventral margin of prosternum flanged, bent or folded caudad away from head, usually bearing a tuft of hair; pronotum usually stouter, anterior margin usually serrate; antennal funicle 3-segmented; monogamous; Mexico to South America; 1.5-3.9 mm . . . . ***Tricolus***

— Posterior margin of elytral declivity strongly to profoundly explanate, weakly to profoundly divaricate; declivital armature variable, often remarkable; antennal club oval to very elongate; anteroventral margin of prosternum fitting snugly against head (not bent caudad), sparsely pubescent; pronotum usually much more elongate, anterior margin variously sculptured, rarely serrate; antennal funicle usually 3-segmented, occasionally 2-segmented; monogamous; Mexico to South America; 2.5-8.0 mm . . . . ***Amphicranus***

22(20). Antennal funicle 4-segmented; frons with median carina; pronotum dimorphic, female with anterior slope strongly declivous, armed by numerous asperities, anterolateral angles each bearing a tuft of hair, male slope gradual, asperities greatly reduced in size and number, anterior margin a strongly formed, slightly produced continuous costa; elytral declivity divaricate from middle, truncated before apex; Asia (Tibet); 2.0 mm . . ***Gnatharus***

— Antennal funicle 2- or 3-segmented; pronotum and elytra quite different; American genera 23

23(22). Elytral apex divaricate, often also explanate; antennal club oval to broadly triangular; lateral margins of pronotum usually with a fine, raised line (a few exceptions); body moderately to very slender; mostly polygynous; North and South America; 1.4-4.8 mm . . . . ***Monarthrum***

— Elytral apex entire, never explanate; lateral margins of pronotum rounded; antennal club more than twice as long as wide (except 1.6 times in male *Metacorthylus*), its apex narrowly rounded; body comparatively stout . . . 24

24(23). Antennal funicle 3-segmented; female frons excavated and elaborately ornamented by long hair; antennal club not sexually dimorphic, elongate, slightly asymmetrical; pronotum and elytral disc glabrous; monogamous; S Mexico to Guatemala; 3.0-3.8 mm . . . . ***Glochinocerus***

— Antennal funicle 2-segmented; frons convex and subglabrous in both sexes; antennal club asymmetrically very elongate in female, elongate-oval in male; pronotum and elytra minutely, closely pubescent; monogamous; Costa Rica to Colombia; 1.9-2.7 mm . . . . ***Metacorthylus***

25(19). Lateral margins of pronotum rounded; elytral disc usually impunctate, declivity short, very steep, narrowly sulcate on basal third, triangularly impressed below, costal margins near apex ascending slightly; antennal club subcircular, syummetrical, with 2 aseptate sutures marked by rows of setae; female frons convex, pubescence inconspicuous; monogamous; Mexico to South America; 1.2-2.4 mm . . . . ***Microcorthylus***

— Lateral margins of pronotum marked by a fine, raised line (except some *Corthycyclon*), elytral disc usually with clearly marked, confused punctures, declivity convex, truncate, or variously sculptured (but not as above); female frons usually moderately to strongly concave, often ornamented by hair; antennal club symmetrical to strongly asymmetrical, sutures present or not 26

26(25). Antennal club aseptate, without sutures (some species with weak, transverse grooves, without rows of setae), usually very elongate; lateral margins of pronotum either with or without a fine, raised line; posterior face of protibia inflated and tuberculate; female frons broadly, evenly concave and ornamented by fine hair; monogamous; Mexico to South America; 1.3-2.4 mm . . . . ***Corthycyclon***

— Antennal club with 1 or 2 sutures, its outline subcircular to strongly asymmetrical (if sutures absent then posterior face of protibia flat, smooth); female frons variable 27

27(26). Elytral apex strongly, obtusely divaricate; female antennal club with 1 septate suture, tapered on apical half to strongly acuminate apex, posterior face of club without a tuft of long hair; female protibia inflated, armed on posterior face; Venezuela; 2.5 mm . . . . *Brachyspartus*

— Elytral apex entire (a small cleft in *Corthylus emarginatus*); female antennal club not tapered or acuminate at apex 27

28(27). Elytral declivity narrowly, weakly sulcate (except uniformly convex in 1 species), lateral margins armed by 2 or 3 pairs of pointed granules; antennal scape elongate, club shaped; female frons variously impressed, with a pair of median carinae narrowly separated by a sulcus over part or all of median line; color pale yellow to yellowish brown; antennal club symmetical, broadly oval, with 2 finely marked sutures; female protibia inflated, posterior face tuberculate; monogamous; Mexico to South America; 1.5-2.8 mm . . . . *Corthylocurus*

— Sculpture of elytral declivity convex, truncately concave, or variously impressed (but never narrowly sulcate); antennal scape subquadrate, stout; female frons never with pair of median carinae; antennal club slightly to profoundly asymmetrical, sutures (when present) rather strongly marked; posterior face of protibia smooth or tuberculate; monogamous; North and South America; 1.2-4.3 mm . . . . *Corthylus*

Corthylini: Pityophthorina

***Mimiocurus* Schedl** [1957a: 72, Type-species: *Mimiocurus acuminatus* Schedl, monobasic. Synonyms: *Micracidendron* Schedl 1957a: 71, Type-species: *Micracidendron montanum* Schedl, monobasic; *Mimiophthorus* Schedl 1957a: 77, Type-species: *Brachydendrulus montanus* Schedl, original designation]. Distribution: About 8 species in Africa, 1 in India, 1 in China.

***Styphlosoma* Blandford** [1904: 232, Type-species: *Styphlosoma granulatum* Blandford, monobasic]. Distribution: 1 species in Central America (Costa Rica to Panama), 3 in South America. They are heterosanguineously polygynous and phloeophagous.

***Dendroterus* Blandford** [1904: 233, Type-species: *Dendroterus mexicanus* Blandford, subsequent designation by Hopkins 1914: 120. Synonyms: *Plesiophthorus* Schedl 1940a: 343, Type-species: *Plesiophthorus perspectus* Schedl, monobasic; *Xylochilus* Schedl 1956: 30, Type-species: *Xylochilus insularis* Schedl =*Dendroterus sallaei* Blandford, original designation]. Distribution: 15 species in North and Central America. All are heterosanguineously polygynous and phloeophagous. Key: Wood (1982: 918).

***Phloeoterus* Wood** [1984: 117, Type-species: *Phloeoterus burserae* Wood, original designation]. Distribution: 1 species in *Bursera* in Mexico.

***Araptus* Eichhoff** [1872: 136, Type-species: *Araptus rufopalliatus* Eichhoff, monobasic. Synonyms: *Neodryocoetes* Eggers 1933a: 9, Type-species: *Neodryocoetes hymenaeae* Eggers, monobasic; *Thamnophthorus* Schedl 1938c: 174, Type-species: *Thamnophthorus volastos* Schedl, subsequent designation by Blackman 1942b: 178; *Neopityophthorus* Schedl 1938c: 180, Type-species: *Pityophthorus laevigatus* Eggers, designated by Wood 1982: 928; *Sphenoceros* Schedl 1939e: 565, Type-species: *Sphenoceros limax* Schedl, monobasic; *Hypertensus* Hagedorn, nòmen nudum (in Schedl 1950d: 164), Type-species: *Hypertensus reitteri*, nomen nudum =*Sphenoceros limax* Schedl, no status; *Brachydendrulus* Schedl 1951b: 114, Type-species: *Brachydendrulus eggersi* Schedl, monobasic; *Gnathocranus* Schedl 1951b: 116, Type-species: *Gnathocranus novateutonicus* Schedl, monobasic; *Gnathoborus* Schedl 1970a: 93, Type-species: *Breviophthorus argentiniae* Schedl, original designation]. Distribution: 53 species in North and Central America, about 50 in South America and adjacent islands. Some are monogamous, some are heterosanguineously polygynous, and at least 3 are consanguineously polygynous (*laevigatus*, *costaricensis*, etc.); most are phloeophagous, a few are spermophagous, and some are myelophagous in vines (lianas). Key: Wood 1982: 928) for North and Central America.

***Conophthorus* Hopkins** [1915c: 430, Type-species: *Pityophthorus coniperda* Schwarz, original designation]. Distribution: 14 species in North America. All species are monogamous and spermophagous in cones of *Pinus*. Key: Wood (1982: 982).

***Pityoborus* Blackman** [1922: 96, Type-species: *Crypturgus comatus* Zimmermann, monobasic]. Distribution: 7 species in North and Central America. All are monogamous and phloeophagous in *Pinus*. Keys: Wood (1958: 47, 1982: 1147).

Dacnophthorus **Wood** [1975: 394, Type-species: *Gnathophthorus clematis* Wood, original designation]. Distribution: 2 species in North and Central America, 2 in South America. All are monogamous and bore in the stems of vines (lianas) (*Clematis* and a species of Bignoniaceae). Key: Wood (1982: 1152) for North and Central America.

Pityotrichus **Wood** [1962: 76, Type-species: *Pityophilus barbatus* Blackman, automatic. Synonym: *Pityophilus* Blackman 1928a: 147, Type-species: *Pityophilus barbatus* Blackman, original designation, preoccupied]. Distribution: 2 species in North America (Arizona, New Mexico). Both are heterosanguineously polygynous and phloeophagous. Key: Wood (1982: 1141).

Gnatholeptus **Blackman** [1943a: 34, Type-species: *Gnatholeptus mandibularis* Blackman =*Pityophthorus shannoni* Blackman, original designation]. Distribution: 4 species in Central and N South America. All are heterosanguineously polygynous and phloeophagous, mostly in *Protium*. The status of this genus should be reviewed. Key: Wood (1982: 1142).

Pityodendron **Schedl** [1953a: 93, Type-species: *Pityodendron madagascarensis* Schedl, monobasic]. Distribution: 1 species in Madagascar.

Sauroptilius **Browne** [1970: 558, Type-species: *Xyleborus sauropterus* Schedl, original designation]. Distribution: 1 species in Madagascar.

Phelloterus **Wood** [1971: 46, Type-species: *Phelloterus tersus* Wood, original designation]. Distribution: 3 species in South America (Colombia to Venezuela). All are heterosanguineously polygynous and phloeophagous.

Spermophthorus **Costa Lima** [1929: 111, Type-species: *Spermophthorus apuleiae* Costa Lima, monobasic]. Distribution: 1 species in Central America (Costa Rica), 2 in South America.

Pseudopityophthorus **Swaine** [1918: 93, Type-species: *Crypturgus minutissimus* Zimmermann, original designation]. Distribution: 23 species in North and Central America, 1 in South America (Colombia), 1 in China. All are bigynous and phloeophagous, mostly in *Quercus*. Keys: Blackman (1931a: 225), Wood (1982: 966).

Pityophthorus **Eichhoff** [1864: 39, Type-species: *Bostrichus lichtensteini* Ratzeburg, subsequent designation by Hopkins 1914: 127. Synonyms: *Trigonogenius* Hagedorn 1912: 354, Type-species: *Trigonogenius fallax* Hagedorn, monobasic; *Hagedornus* Lucas 1920: 683, Type-species: *Trigonogenius fallax* Hagedorn, automatic; *Myeloborus* Blackman 1928a: 16, Type-species: *Pityophthorus ramiperda* Swaine, original designation; *Gnathophorus* Schedl 1935: 342, Type-species: *Gnathophorus sparsepilosus* Schedl, monobasic, preoccupied; *Conophthocranulus* Schedl 1935: 343, Type-species: *Conophthocranulus blackmani* Schedl, monobasic; *Breviophthorus* Schedl 1938c: 176, Type-species: *Breviophthorus brasiliensis* Schedl, monobasic; *Pityophthoroides* Blackman 1942b: 199, Type-species: *Pityophthoroides pudens* Blackman, original designation; *Cladoborus* Sawamoto 1942: 165, Type-species: *Cladoborus arakii* Sawamoto, monobasic; *Neomips* Schedl 1954a: 37, Type-species: *Neomips brasiliensis* Schedl =*Pityophthorus dimorphus* Schedl, monobasic; *Ctenyophthorus* Schedl 1955b: 26, Type-species: *Ctenyophthorus glabratulus* Schedl, mono-basic; *Gnathophthorus* Wood 1962: 76, Type-species: *Gnathophorus sparsepilosus* Schedl, automatic; *Hypopityophthorus* Bright 1981a: 14, Type-species: *Pityophthorus inops* Wood, original designation]. Distribution: 225 species in North and Central America, about 100 in South America and adjacent islands, about 15 in Asia, 22 in Europe, 22 in Africa. Most are heterosanguineously polygynous, a few are monogamous; most are phloeophagous, a few are myelophagous. Keys: Pfeffer (1976: 334) for Europe, Blackman (1928a), Bright (1981a), and Wood (1982: 991) for North and Central America.

Corthylini: Corthylina

Gnathotrichus **Eichhoff** [1869: 275, Type-species: *Gnathotrichus corthyloides* Eichhoff *Tomicus materiarius* Fitch, monobasic. Synonyms: *Gnathotrichoides* Blackman 1931b: 267, Type-species: *Cryphalus sulcatus* LeConte, subsequent designation by Wood 1982: 1155; *Ancyloderes* Blackman 1938b:205, Type-species: *Cryphalus pilosus* LeConte, original designation; *Paraxyleborus* Hoff-

mann 1942: 72, Type-species: *Xyleborus duprezi* Hoffmann =*Tomicus materiarius* Fitch, monobasic; *Prognathotrichus* Bright 1972: 1678, Type-species: *Prognathotrichus primus* Bright, original designation]. Distribution: 13 species in North and Central America. All are monogamous and xylomycetophagous. Keys: Blackman (1931b: 266), Wood (1982: 1156).

***Gnathotrupes* Schedl** [1951b: 125, Type-species: *Gnathotrupes bolivianus* Schedl, monobasic. Synonyms: *Gnathotrypanus* Wood 1968a: 9, Type-species: *Gnathotrypanus terebratus* Wood, original designation; *Gnathocortus* Schedl 1975a: 11, Type-species: *Gnathocortus caliculus* Schedl, original designation; *Gnathomimus* Schedl 1975a: 12, Type-species: *Gnathomimus nothofagi* Schedl, original designation; *Gnathoglochinus* Schedl 1975a: 16, Type-species: *Gnathoglochinus impressus* Schedl, original designation]. Distribution: 5 species in Central America, about 30 in South America. All are monogamous and xylomycetophagous. Key: Wood(1982: 1167) for Central America.

***Tricolus* Blandford** [1905: 286, Type-species: *Tricolus ovicollis* Blandford, subsequent designation by Hopkins 1914: 131. Synonym: *Pterocyclonoides* Schedl 1970a: 101, Type-species: *Pterocyclonoides octodentatus* Schedl, monobasic]. Distribution: 24 species in North and Central America, about 17 in South America. All are monogamous and xylomycetophagous. Key: Wood (1982: 1170) for North and Central America.

***Amphicranus* Erichson** [1836: 63, Type-species: *Amphicranus thoracicus* Erichson, monobasic. Synonyms: *Piezorhopalus* Guerin-Meneville 1838: 107, Type-species: *Piezorhopalus nitidulus* Guerin-Meneville =*Amphicranus thoracicus* Erichson, monobasic; *Steganocranus* Eichhoff 1878a: 460, Type-species: *Steganocranus dohrni* Eichhoff, monobasic]. Distribution: 29 species in North and Central America, about 23 in South America. All are monogamous and xylomycetophagous; apparently some appropriate the tunnel of another species of Scolytidae or Platypodidae by driving out or killing the original occupants (domicile parasitism). Key: Wood (1982: 1186) for North and Central America.

***Gnatharus* Wood & Yin** [1986: 463, Type-species: *Gnatharus tibetensis* Wood & Yin, original designation]. Distribution: 1 species in Asia (Tibet).

***Monarthrum* Kirsch** [1866: 213, Type-species: *Monarthrum chapuisi* Kirsch, monobasic. Synonyms: *Corthylomimus* Ferrari 1867: 48, Type-species: *Bostrichus fasciatus* Say, subsequent designation by Hopkins 1914: 118; *Cosmocorynus* Ferrari 1867: 62, Type-species: *Cosmocorynus cristatus* Ferrari, monobasic; *Pterocyclon* Eichhoff 1869: 276, Type-species: *Pterocyclon laterale* Eichhoff, subsequent designation by Hopkins 1914: 128, neotype for type-species designated by Wood 1966: 25; *Anchonocerus* Eichhoff 1878a: 67, 431, Type-species: *Anchonocerus rufipes* Eichhoff, monobasic; *Phthorius* Eichhoff 1878a: 67, 433, Type-species: *Phthorius ingens* Eichhoff, monobasic; *Trypocranus* Eichhoff 1878a: 67, 435, Type-species: *Trypocranus cincinnatus* Eichhoff, monobasic; *Eupteroxylon* Eggers 1936a: 392, Type-species: Type-species: *Eupteroxylon comatum* Eggers, monobasic]. Distribution: 58 species in North and Central America, about 78 in South America and adjacent islands. Most species are heterosanguineously polygynous, a few small species are monogamous; all are xylomycetophagous. Key: Wood (1982: 1207) for North and Central America.

***Glochinocerus* Blandford** [1904: 266, Type-species: *Glochinocerus retusipennis* Blandford, subsequent designation by Hopkins 1914: 122]. Distribution: 2 species in Mexico (Hidalgo) and Central America (Guatemala). Both are monogamous and xylomycetophagous. Key: Wood (1982: 1246).

***Metacorthylus* Blandford** [1904: 251, 263, Type-species: *Metacorthylus nigripennis* Blandford, monobasic. Synonym: *Paracorthylus* Wood 1968a: 7, Type-species: *Paracorthylus velutinus* Wood, original designation]. Distribution: 4 species in Central America 1 of which also occurs in South America (Colombia). All are apparently monogamous and xylomycetophagous. Key: Wood (1982: 1248).

***Microcorthylus* Ferrari** [1867: 58, Type-species: *Microcorthylus parvulus* Ferrari, monobasic]. Distribution: 13 species in Mexico and Central America, 19 in South America. All are monogamous and xylomyce-

tophagous. Key: Wood (1982: 1252) for North and Central America.

***Corthycyclon* Schedl** [1951b: 128, Type-species: *Corthycyclon ustum* Schedl, monobasic]. Distribution: 6 species in Mexico and Central America, about 10 in South America. All are monogamous and xylomycetophagous. Key: Wood (1982: 1260) for North and Central America.

***Brachyspartus* Ferrari** [1867: 65, Type-species: *Brachyspartus moritzi* Ferrari, monobasic. Synonym: *Thylurcos* Schedl 1939e: 567, Type-species: *Brachyspartus moritzi* Ferrari, subsequent monotypy (Wood 1982: 1298). Distribution: 1 species in South America (Venezuela).

***Corthylocurus* Wood** [1966: 18, Type-species: *Brachyspartus barbatus* Blandford, original designation]. Distribution: 6 species in Mexico and Central America, about 8 in South America. All are monogamous and xylomycetophagous. Key: Wood (1982: 1265) for Mexico and Central America.

***Corthylus* Erichson** [1836: 64, Type-species: *Bostrichus compressicornis* Fabricius, subsequent monotypy (Ferrari 1867: 49), lectotype designated for type-species by Wood 1974: 202. Synonyms: *Morizus* Ferrari, 1867: 69, Type-species: *Morizus excisus* Ferrari, monobasic; *Pseudocorthylus* Ferrari 1867: 59, Type-species: *Pseudocorthylus letzneri* Ferrari, subsequent designation by Hopkins 1914: 128]. Distribution: 56 species in North and Central America, about 54 species in South America. All are monogamous and xylomycetophagous. Key: Wood (1982: 1271) for North and Central America.

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